# Journal of the Royal Society of Western Australia

CONTENTS

Volume 77   Part 1
March 1994

The Royal Society of Western Australia

To promote and foster science in Western Australia

PATRON

Her Majesty the Queen

VICE-PATRON

His Excellency Major General Michael Jeffrey AO MC
Governor of Western Australia

COUNCIL 1993-94

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JOURNAL OF THE ROYAL SOCIETY OF WESTERN AUSTRALIA

CONTENTS   VOLUME 77   PART 4, DECEMBER 1994

Plant Diseases in Ecosystems:
Threats and impacts in south-western Australia

Recent Advances in Science in Western Australia

Earth Sciences

W K Witt of the Geological Survey of Western Australia, Perth, describes how the Menzies-Kambalda region has produced 1700 tonnes of gold, with most production accounted by mafic rocks, especially Fe-rich basalt and differentiates of fractionated sills. Mineralization occurs in diverse structural settings, related to the latest stages of regional deformation or emplacement of comtemporaneous granitoid intrusions, that were active during gold-related hydrothermal activity.

Witt W K 1993 Gold mineralization in the Menzies-Kambalda region, Eastern Goldfields, Western Australia. Geological Survey of Western Australia. Report 39.

Two iridium anomalies have been identified by R S Nicoll (AGSO Canberra) and P E Playford (GSWA Perth) near the Frasnian-Famennian boundary in the Canning Basin reef complexes, one above and one below the actual boundary; neither were associated with the extinction event in the *Palmatolepis linguifirmis* Zone. The anomalies were associated with beds containing abundant *Frutexites* microstromatolites, indicating that the iridium was probably organically concentrated, rather than being associated with an impact event.

Nicoll R S & Playford P E 1993 Upper Devonian iridium anomalies, conodont zonation and the Frasnian-Famennian boundary in the Canning Basin, Western Australia. Palaeogengraphy, Palaeoclimatology, Palaeoecology 104:105-113

Coworkers from Durham and Oxford (U. K.) used laboratory studies of quantifiable rock geotechnical parameters to understand slope form and development. Highly concave slopes have formed in limestone, which has little deformation before yield, whereas convexo-concave slopes are characterized by material with a greater strain before yield, a relatively low modulus of elasticity, and a pronounced discontinuity pattern.

Allison R J, Goudie, A S, & Cnx N J 1993 Geotechnical properties of rock masses: their control nn slnpe for, and mechanisms of change along the Napier Range, Western Australia. Geomorphology 8:65-80

A simplified scheme is presented by J R Vearncombe, of the University of Western Australia, to categorize quartz vein morphology from gold deposits, based on the growth direction of quartz or pseudomorphed chalcedony in the veins, into seven types; face-control, displacement-control, parallel-control, radiating, non-directional-control, replacement, and modified. Crustal depth is a major control in the Yilgarn Craton deposits, with parallel and radiating textures near the surface, displacement and non-directional typical of mid-crustal, frontal from near surface to midcrustal, and replacement and modified at all crustal levels.

Veanncombe J R 1993 Quartz vein morphnlogy and implications for formation depth and classification of Archean gold-vein deposits. Ore Geolngy Reviews 8:407-424

Ten articles concerning a variety of topics have been published in the latest Professional Paper volume of the Geological Survey of Western Australia, including five of hydrogeological interest; Salinity control at Lake Toolibin (M W Martin); Hydrogeology of the Cervantes-Lancelin Region (A M Kern); Point sources of groundwater contamination in the Perth Basin (K-J Hirschberg); Municipal waste disposal in Perth and its impact on groundwater quality (K-J Hirschberg); Hydrogeology of the Collie Basin (J S Moncrieff).

Professional Papers. Geolngical Survey nf Western Australia. Report 34

Life Sciences

A survey of the tick load in natural populations of sleepy lizards in South Australia, by M. Bull and D Burzacott of Flinders University, showed that lizards do not appear to be adversely affected by high tick loads, as neither size nor longevity was negatively correlated with tick load, and mating pairs had higher tick loads than non-mating individuals.

Bull C M & Burzacott D 1993 The impact of tick load on the fitness of their lizard hosts. Oecologia 96:415-419

The diets of arid zone dasyurid marsupials are shown by D Fisher and C Dickman, of the University of Sydney, to consist primarily of beetles, spiders, scorpions and centipedes. Small dasyurids avoided beetles with hard cuticles, and generally preferred prey 5 to 7.5 mm long over smaller (<2.5 mm) prey.

Fisher D O & Dickman C R 1993 Diets nf insectivorous marsupials in arid Australia: selection fnr prey type, size or hardness? Journal of Arid Envirnnments 25:397-410

The pattern of torpor of the Eastern pygmy possum was shown by F Geiser of the University of New England to be regular in the laboratory, with increasing occurrence at lower air temperatures. The duration of torpor lengthened with lower air temperature, to about 17 days at 5 C, and the minimum metabolic rate declined to less than 2% of the basal rate.

Geiser F 1993 Hibernation in the Eastern pygmy possum, *Cercartetus nanus* (Marsupialia: Burramyidae). Australian Journal of Zoology 41:67-75

A model of water regulatory efficiency developed for granivorous parrots by R MacMillen, of the University of California at Irvine, and R Baudinette of Flinders University, suggests that small size imparts a higher water efficiency, but requires them to rely on small seeds rich in carbohydrates, as these provide maximal yields of metabolic water.

MacMillen R E & Baudinette R V 1993 Water economy of granivorous birds: Australian parrots. Functional Ecnlngy 7:704-712

The collembolan faunas of rehabilitated bauxite mines are shown by P Greenslade (CSIRO, Canberra) and J Majer (Curtin University) to have increased species richness in larger plots, with greater plant species richness and percentage plant cover; their results provide directions for improving rehabilitation practices.

Greenslade P & Majer J D 1993 Recolonization by Collembola of rehabilitated bauxite mines in Western Australia. Australian Journal of Ecology 18:385-394

The standard metabolic rate of Western Australian frogs was shown by P Withers of the University of Western Australia to be similar to that predicted for other anurans. Species of *Neobatrachus* and *Cyclorana* had a depressed metabolic rate (to 20-30% of standard) during aestivation.

Withers P C 1993 Metabolic depression during aestivation in the Australian frogs, *Neobatrachus* and *Cyclorana*. Australian Journal of Zoology 41:467-473

Physical Sciences

Chemists from the School of Mathematical and Physical Sciences at Murdoch University have developed a potentiometric titration method and determined copper (I) equilibrium constants in aqueous solution for cyanide and D-penicillamine complexes. The copper (I) solutions are prepared by reduction of the common copper (II) state with excess copper metal, and are stabilised by chloride.

Hefter, G T, May P M & Sipos P 1993 A general method for the determination of copper (I) equilibria in aqueous solution. Journal of the Chemical Society Chemical Communications:1704-1706

An experimental and theoretical study, by physicists of the University of Western Australia and Murdoch University, of the angular correlations of sequential cascading photons in an atomic hydrogen system with a defined scattering plane demonstrates that the measured correlations and the deduced multiple moments show an order-of-magnitude agreement with various theoretical models.

Williams J F, Kumar M & Stelbovics A T 1993 Angular correlations between sequential cascading photons from n=3 atomic hydrogen. Physical Review Letters 70:1240-1243

Polarized neutron diffraction experiments at low temperatures in a high magnetic field have been used by researchers at the University of Western Australia, the Royal Institution (UK) and the Institut Laue-Langevin (France) to study the anisotropy of the orbital moment of the low spin hexacyanoferrate (III) ion. The data are consistent with a cubic crystal field model in which the magnetization is dominated by the orbital moment.

Day P, Delfs C D, Figgis B N, Reynolds P A & Tasset F 1993 Polarized neutron diffraction from $Cs_2KFe(CN)_6$ Molecular Physics 78:769-780

The structure of hydrogenated amorphous silicon, an important photovoltaic material, has been modelled by hypothetical silane molecules with diamond or similar lattices using the semi-empirical quantum mechanical AM1 method by scientists at Murdoch University. Densities of states and infrared spectra were calculated and compared with experimental data.

Clare B W, Jennings P J, Cornish J C L, Talukder G, Lund C P & Hefter G T 1993 Simulation of the electronic and vibrational structure of hydrogenated amorphous silicon using cluster models. Journal of Computational Chemistry 14:1423-1428

Note from the Hon Editor: This column helps to link the various disciplines and inform others of the broad spectrum of achievements of WA scientists (or others writing about WA).

Contributions to "Recent Advances in Science in Western Australia" are welcome, and may include papers that have caught your attention or that you believe may interest other scientists in Western Australia and abroad. Papers in refereed journals, or books, chapters and reviews will be accepted. Abstracts from conference proceedings will not be accepted. Please submit short (2-3 sentences) summaries of recent papers, together with a copy of the title, abstract and authors' names and addresses, to the Honorary Editor (c/o Western Australian Museum) or a member of the Publications Committee: Dr S D Hopper (Life Sciences), Dr A E Cockbain (Earth Sciences), and Assoc. Prof. G Hefter (Physical Sciences). Final choice of articles is at the discretion of the Hon Editor.

"Letters to the Editor" concerning scientific issues of relevance to this journal are also published at the discretion of the Hon Editor. Please submit a word processing disk with letters, and suggest potential reviewers or respondents to your letter. *PC Withers, Hon Editor, Journal of the Royal Society of WA*

The Royal Society of Western Australia

Medal Recipients

1924-1993

The Medal of the Royal Society of Western Australia was instituted in 1924 to mark the centenary of the birth of Lord Kelvin (26 June, 1824). The Royal Society Medal (originally referred to as the "Gold Medal" and then subsequently sometimes as the "Kelvin Medal" due to the association of the inaugural award with the centennial Kelvin celebration and because the medal bears in relief on its obverse side the head of Kelvin) is awarded approximately every four years for distinguished work in science connected with Western Australia. The original dye for the medal, first struck in 1924, remains in the safe-keeping of the Society. The first three medals were struck in gold, and all subsequent medals in silver. The first medallist of the Royal Society was Dr William J. Hancock, Government Electrical Engineer and Honorary Medical Radiographer at Perth Hospital, who in 1924 was the recipient of the Medal of the Royal Society of Western Australia, in recognition of his pioneering work in the medical application of X-rays. The most recent medallist, Professor John R. de Laeter, was presented with the seventeenth Medal of the Royal Society of Western Australia, in recognition of his contributions to geophysics and geochronology.

Recipients of the Royal Society Medal of Western Australia are:
(reference to Journal of the Royal Society notice of medal award in parentheses)

1924	Dr W J Hancock: radiography; medical application of X-rays (10:xvii)
1929	Dr E S Simpson: mineralogy and geology of Western Australia (15:iv)
1933	Mr W M Carne: plant pathology; the bitter pit of apples (19:xi)
1937	Mr A Gibb Maitland: geology; Pilbara survey and artesian water supplies (23:xi)
1941	Prof E de C Clarke: geology of Western Australia (27:v)
1945	Mr L Glauert: natural sciences (31:vi)
1949	Mr C A Gardner: botany; the flora of Western Australia (35:v)
1955	Dr H W Bennetts: veterinary science; live stock diseases (40:1)
1959	Prof E J Underwood: animal nutrition and husbandry (43:67)
1966	Mr C F H Jenkins: agricultural entomology and natural history (49:91)
1970	Prof R T Prider: geology; petrology and mineralogy (53:95)
1979	Prof R M Berndt: anthropology; aborginal studies (63:29)
1979	Emer Prof B J Grieve: botany; ecophysiology and the flora of WA (63:29)
1979	Dr D L Serventy: zoology; ornithology and nature conservation (63:29)
1983	Dr J S Beard: botany; vegetation classification and mapping (65:93)
1986	Prof C A Parker: soil biology
1993	Prof J R De Laeter: geophysics and geochronology (77:4)

The Royal Society of Western Australia Medallist, 1993.

John de Laeter, AO CitWA, BSc(Hons), BEd(Hons), PhD, DSc(WA), FTS, CPhys, FInstP, Hon FAIP, Professor of Physics, Deputy Vice-Chancellor, and Dean of Graduate Studies, Curtin University of Technology.

The Medallist for 1993, Professor John de Laeter, AO Cit WA, BSc(Hons), BEd(Hons), PhD, DSc(West Aust), FTS, CPhys, FInstP, Hon FAIP, Professor of Physics, Deputy Vice-Chancellor of Research and Development and Dean of Graduate Studies at Curtin University of Technology, was elected by the Council of the Royal Society of Western Australia because of his contributions to the scientific knowledge of the geophysics of Western Australia. The Medal was presented at the Inaugural Royal Society of Western Australia Medal Lecture by His Excellency the Governor of Western Australia, Major General Michael Jeffrey, AO MC, Vice-Patron of the Royal Society of Western Australia, on Monday 8 November, 1993.

Professor John R. de Laeter was born at South Perth in 1933, and educated at Perth Modern School and The University of Western Australia from which he holds First Class Honours degrees in Physics and Education, and Doctorates in Philosophy and Science. He is a Fellow of the Australian Academy of Technological Sciences and Engineering, and the Australian and British Institutes of Physics. He is presently a member of the Board of CSIRO, the Higher Education Council, the Research Training and Careers Committee, and the Institutional Grants Committee of the Australian Research Council. He has held visiting research appointments at McMaster University in Canada, the Australian National University, Pennsylvania State University, Cambridge University, and the Central Bureau of Nuclear Measurements in Belgium. He is past chairman of the Commission of Atomic Weights and Isotope Abundances, and is a member of the Council of the Inorganic Chemistry Division of the International Union of Pure and Applied Chemistry.

His major research interest is the application of mass spectrometry to a range of astrophysical, chemical, geological and nuclear problems. He has played a major role in the development of geochronology in Western Australia, in analysing Western Australian meteorites, in radioactive waste containment studies, and in the accurate determination of the isotopic abundances of numerous elements, many of which led to new values of their atomic weights. He has a long-standing interest in nuclear astrophysics and the origin of the chemical elements. He is also recognised as a science educator, with a particular concern for ensuring that the public is informed of the role of science and technology in society. He was one of the key persons involved in the concept of the Scitech Discovery Centre in Perth, and presently serves as Deputy Chairman of the Board. His other major concern has been to improve the relationship between Universities, Government and industry, and was instrumental in the establishment of Technology Park, adjacent to Curtin University, where he serves as Chairman of the Advisory Board.

Professor de Laeter received the ANZAAS Medal in 1992.

A question of time: Royal Society Medallist's Lecture for 1993

J R De Laeter

Department of Applied Physics, Curtin University of Technology,
Perth, Western Australia, 6001

The cheeseboard is the world, the pieces are the phenomena of the universe, the rules of the game are what we call the laws of nature. The player on the other side is hidden from us. We know that his play is always fair, just, and patient. But also we know, to our cost, that he never overlooks a mistake, or makes the smallest allowance for ignorance.

T H Huxley, 1868
A Liberal Education

Introduction

I am honoured that the Royal Society of Western Australia has conferred on me the Royal Society Medal for 1993. As a member and Past President of the Society, I am pleased that my colleagues have seen fit to recognise my research, which has almost in its entirety been carried out in Western Australia, first at the University of Western Australia, then at the Western Australian Institute of Technology and subsequently at Curtin University. I dedicate this lecture to my wife and family and research colleagues who have made this award possible. I would also like to thank His Excellency, the Governor of Western Australia, Major General Michael Jeffrey, for presenting the Royal Society medal to me on the occassion of this lecture.

I have chosen "**A Question of Time**" as my topic for this Medallist's address, and I would like to explore with you some of the questions which all of us have asked:-

How old is the Universe?
How long did the Sun take to form?
How old is the Solar System?
How old is this rock?

The concept of time has never ceased to intrigue and puzzle those who think about it. We instinctively feel that time goes on unceasingly, and that there is nothing we can do to halt its inexorable progress. However, Albert Einstein has taught us that time is not immutable; rather it is relative and depends on the observer. I wish to consider time as the order in which events occur. How then are we to measure geological time?

For centuries various people tried to estimate the age of the Earth by heat flow (Lord Kelvin), by tidal interaction (George Darwin), by the saltiness of the oceans (Edmond Halley) and by the accumulation of sediments (Charles Walcott). However, none of these "clocks" was particularly accurate, and the physicist Lord Kelvin fell into disrepute with geologists because his estimated age of 10 million years, which he obtained by examining the cooling of the Earth from a molten body, was far too short as far as the geologists were concerned.

Then in 1896 came the breakthrough that was needed to measure geological time. Henri Becquerel discovered that certain minerals were radioactive, and Marie and Pierre Curie then showed that these radioactive atoms change into other atoms at regular and constant rates. After a certain period of time, exactly half the radioactive parent atoms decay to daughter atoms - this period is the half-life of the radioactive parent. Provided one knows the value of the half-life and the proportion of parent to daughter atoms, we can calculate the period of time over which the parent has been decaying, subject to the fact that the system has been "closed" over the time interval concerned.

In 1902 two scientists at McGill University in Canada, the New Zealand physicist Ernest Rutherford and the English chemist Frederick Soddy, investigated the radioactive decay of uranium and showed that it decayed to a daughter product (lead) and also produced helium from the alpha particles emitted. In 1905 in the Silliman lectures at Yale, Rutherford suggested the possibility of using radioactivity as a geological timekeeper, on the basis that if one could measure either of the daughter products helium or lead, then one could measure geological time by this uranium nuclear clock (Rutherford, 1906).

Unfortunately the only means available at that time to measure helium and lead were chemical techniques, and both suffered from serious shortcomings. Helium, being a gas, leaked out of uranium-rich ores, especially if they were weathered, and thus the calculated ages were very much minimum estimates. The measurement of the quantity of lead could not distinguish the daughter-product lead from primordial lead, and so calculated ages were overestimated.

In the early part of this century, before the establishment of the University of Western Australia, Perth Technical College offered undergraduate degrees in science, in collaboration with the University of Adelaide. In 1904 a group of Western Australians, in an endeavour to gain support for a University, persuaded Frederick Soddy who by then was based in England, to make the long sea-voyage to Australia during his University vacation to give a series of lectures in Perth, Fremantle and Kalgoorlie on the latest scientific results. One of Soddy's lectures concerned radioactivity and the determination of the age of the Earth.

He argued that Kelvin's estimate of the age of the Earth was "absolutely wrong", and postulated that the Earth was heated by the energy released by radioactive decay (Jenkin 1985).

E S Simpson, who in 1904 was Chemist and Assayer of the Geological Survey of WA, took a keen interest in Soddy's lectures. Simpson later became the President of the Royal Society of WA and was awarded the Royal Society Medal in 1929. In 1910 Simpson received samples of a bright-yellow uranium mineral from a pegmatite at Wodgina in the Pilbara. He named it "Pilbarite", measured the amount of helium in it, and calculated its age to be 13 Ma although he pointed out that this age was of no significance due to helium leakage (Simpson 1910). He also chemically analysed two other minerals from the same pegmatite which he identified as mackintoshite and thorogummite. Although Simpson measured the amount of lead in these minerals, he did not publish their ages and it was not until 15 years later that Professor L A Cotton, a geologist at the University of Sydney, used Simpson's analytical data to calculate the uranium-lead ages of these three minerals (Cotton 1926). These published ages were 1475, 1460 and 3840 Ma for the mackintoshite, thorogummite and pilbarite specimens respectively. Holmes & Lawson (1927) revised Cotton's calculations, and an age of 1260 Ma for the mackinstoshite sample was included in a popular book in the same year (Holmes 1927). This was the oldest age recorded in Holmes' book, and so the widespread belief arose that Western Australia possessed the Earth's oldest material.

It is amazing to think that in 1910, a few years after the discovery of the uranium nuclear clock by Rutherford, that a Western Australian scientist should have measured the age of a Pilbara mineral. However, Simpson did not maintain his interest in age determinations, and in a letter in 1927 politely rejected a suggestion from Sir Douglas Mawson, the Antarctic geologist, that he should continue such work.

Mass spectrometry and the modern era of geochronology

The chemical method of determining uranium-lead ages was fraught with many errors, and little progress was made in refining such ages until the discovery of isotopes by J J Thomson at the Cavendish Laboratory at Cambridge in 1912. F W Aston, using a vastly improved mass spectrometer, was able to show that lead had at least three isotopes. In 1929, he showed that a uranium-rich sample of broggerite was highly enriched in ^{206}Pb, and calculate on age of ^{909}Ma (Aston 1929). This heralded a new era in geochronology, based on physical rather than chemical methods. Since that time, the mass spectrometer has become the tool of every practising geochronologist - a veritable time machine which enables us to explore the past. An even more significant conclusion from Aston's isotopic results was drawn by Rutherford, who calculated the age of the Earth to be 3.4 x 10⁹y (Rutherford 1929). This marked the advent of cosmochronology.

In 1940, Alfred O Nier of the University of Minnesota designed a simple mass spectrometer which could measure the isotope abundances of elements with good accuracy (Nier, 1940). His sector field mass spectrometers are now common in geochronological laboratories around the World. He has rightly been called the "father of modern mass spectrometry". Nier was able to calculate a U-Pb age of

2570±70 Ma for a monazite (Nier *et al.* 1941), and later pioneered the K-Ar geochronological technique (Aldrich & Nier 1948).

A mass spectrometer measures the relative abundances of the isotopes of an element by separating the various masses in a transverse magnetic field (Fig 1). The sample is mounted on a filament in the ion source of the mass spectrometer. Thermal energy ionises the atoms, and the resulting positive ions are accelerated from the source into the magnet, and subsequently the dispersed ions are collected in a detector. Varying the magnetic field enables ions of different mass to be brought to a focus in the detector, and hence the relative isotopic abundances of the element in the particular sample can be measured.
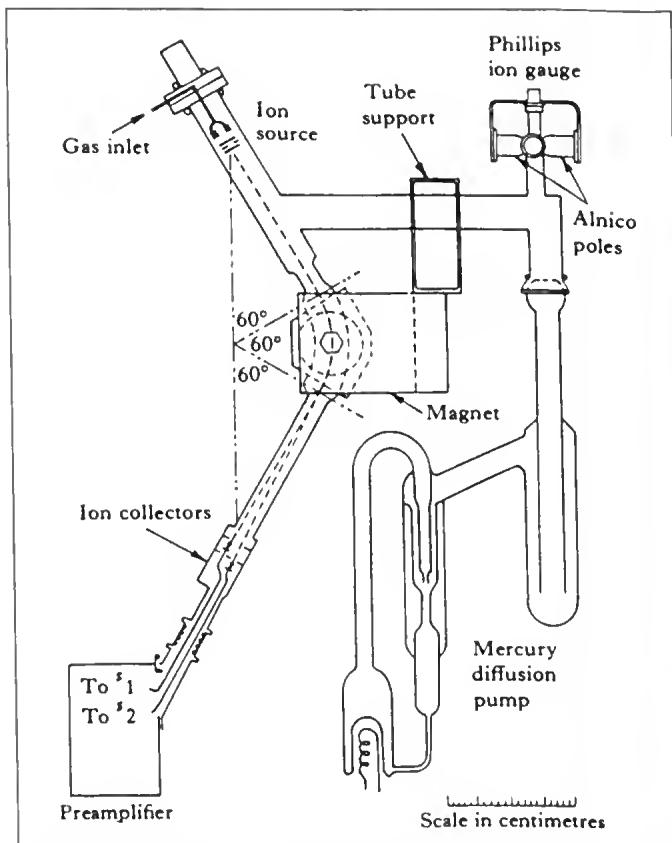
Figure 1. Schematic diagram of a Nier 60 magnetic sector mass spectrometer showing the ion source, magnet and collector assembly.

The Physics Department at the University of Western Australia

In the late 1940's two young physics lecturers at the University of Western Australia (UWA) - Peter Jeffery and Hilary Morton - were building a small nuclear accelerator. On his way to take up a foundation position at the Australian National University (ANU), Sir Marcus Oliphant visited the Physics Department and suggested to Jeffery and Morton that they should build a mass spectrometer and initiate a geochronological research program. Oliphant was a student of Rutherford and was familiar with the physical technique used in geochronology. He referred to the widespread belief that Western Australia contained the Earth's oldest minerals, and that geochronology would be a good field of research for the University to undertake.

Jeffery and Morton built a mass spectrometer out of copper tubing and other odds and ends, but by 1953 had decided to abandon the project unless financial support could be found. Morton in fact left Perth to go to ANU, but Jeffery persevered with a grant from the Carnegie Geophysical Institute in Washington, DC. Jeffery (1976) describes the effect of these funds in the following terms:

> "The Carnegie funds provided the Perth group with a new sixty degree Nier-type mass spectrometer and also permitted the original home-made spectrometer to be upgraded by the replacement of its waterpipe sections with fabricated stainless steel. Such exotic devices as a chart recorder to replace a wall galvanometer, and commercial diffusion pumps were all very acceptable. In spite of these improvements in equipment however, ion currents were still being measured using 'acorn' 954s as electrometers"

I joined the mass spectrometry group at UWA in 1954 as an honours student in physics, and worked with Peter Jeffery and a PhD student - Bill Compston - on carbon isotopes using the "copper tube" mass spectrometer. I was fortunate to be a co-author of the first paper ever published by the mass spectrometry group which described this work (Jeffery *et al.* 1955). The second machine was commissioned by another PhD student, David Greenhalgh in 1955, and the first U-Pb age date was published in 1959 (Greenhalgh & Jeffery 1959).

Peter Jeffery spent 1955 at the Carnegie Institute in Washington DC, and on his return commenced a program of Rb-Sr dating. Bill Compston, who had subsequently completed a Postdoctoral Fellowship at the California Institute of Technology (Cal Tech), became a lecturer in Physics at UWA, and they were joined by a PhD student (Glen Riley) to develop the Rb-Sr technique - which is based on the decay of the radioactive parent ^{87}Rb to the stable daughter ^{87}Sr. The half life of ^{87}Rb is 4.88 x 10^{10}y, and this chronometer is therefore ideally suited for old rocks.

Towards the end of the 1950's, the validity of the Rb-Sr method was being questioned since mineral separates from whole rock samples gave different results. A granite from the Boya quarry was analysed to give ages of 2430 Ma for the whole rock specimen, 650 Ma for the biotite, and 1290 Ma for the microcline extracted from the sample. Compston & Jeffery (1959) argued that the mineral separates had lost a proportion of their radiogenic 87Sr some time after crystallisation, presumably through a metamorphic event, but that the 87Sr was not lost to the whole rock and was simply redistributed within it.

Dr Alan Wilson from the Geology Department at UWA joined forces with Jeffery, Compston, Greenhalgh and Riley to exploit these geochronological techniques in the southern Yilgarn Block and the Albany Fraser Province. A paper by the group in 1960 reported 36 Rb-Sr, 16 K-Ar and 21 U-Pb ages (Wilson *et al.* 1960). The collaboration of physicists and geologists represented an important advance, in that the combined talents of field geologists and laboratory physicists were available to tackle this new field of scientific research which was of enormous potential value to mineral exploration in this State.

After the success of the 1950s, one might have assumed that the University of Western Australia would have become one of the world's leading centres for geochronology, situated as it was in a mineral-rich State with extensive Precambrian terrains. This was not the case. By 1961, the geochronological

program at UWA was non-existent. Bill Compston took up a position at ANU, Glen Riley went to the Australian Institute of Nuclear Science and Engineering, Alan Wilson moved to Queensland, David Greenhalgh became a science teacher, and Peter Jeffery developed new interests in nuclear astrophysics in cooperation with John Reynolds at the Physics Department in the University of California at Berkeley. When Dr Jeffery returned to Perth in 1962, I became his first PhD student in nuclear astrophysics.

Geochronology at the Western Australian Institute of Technology

On my appointment as Inaugural Head of the Department of Applied Physics at the Western Australian Institute of Technology (WAIT) in 1968, after a Post Doctoral fellowship at McMaster University in Canada, a research program to search for isotopic anomalies in meteorites was established using a 30cm radius of curvature solid source mass spectrometer. In late 1968, Dr Alec Trendall of the Geological Survey of Western Australia (GSWA) and Bill Compston argued that some mass spectrometer time should be devoted to geochronology, because of the necessity to place time constraints on the rock units being mapped by geologists at the GSWA, and the inability of Compston's ANU laboratory to handle the immense amount of work that needed to be done. The Rb-Sr technique was chosen because it was relatively simple and ideally suited to the old Archaean rocks which constituted a major portion of the State, and which was the focus of much of the geological mapping at that time. The first geochronological paper from the WAIT laboratory was published in 1970 (De Laeter & Trendall 1970).

In the early 1970s we decided to develop a new geochronological technique based on the decay of ^{176}Lu to ^{176}Hf, with a half life of 3.54 x 10^{10}y. Although the mass spectrometry of hafnium presents some difficulties, the Lu-Hf chronometer has some characteristics which made it an attractive research project. However, our interests were diverted from geochronology to cosmochronology and thus the Lu-Hf geochronometer was not developed at that time (McCulloch *et al.* 1976). Malcolm McCulloch later was instrumental in developing the Sm-Nd geochronological technique at Cal Tech (McCulloch & Wasserburg 1978a), before taking an appointment at ANU.

The Sm-Nd technique is based on the decay of ^{147}Sm to ^{143}Nd with a half life of 10.6 x 10^{10}y. As parent and daughter are both rare earth elements, natural fractionation processes do not favour a separation as occurs for many pairs of elements used in geochronology. This technique was introduced at WAIT in 1979 (Fletcher & Rosman 1980), and has been used successfully to solve a number of geochronological problems.

By the mid-1970s, geochronology was a major component of the work of the mass spectrometer laboratory at WAIT. In 1974 geologists from the University of Western Australia became associated with the mass spectrometry laboratory, and an extensive survey of Yilgarn ages was carried out using the Rb-Sr technique. With the appointment of Dr M T Bickle to the Geology Department of UWA in 1979, the tempo of the geochronology program accelerated, and a

number of articles have subsequently been published on the Yilgarn Block (Chapman *et al.* 1981) and on the Pilbara Block (Bickle *et al.* 1983). A U-Pb chemical extraction laboratory was established at UWA, and the U-Pb and Pb-Pb geochronological techniques complemented the existing Rb-Sr and Sm-Nd techniques.

The appointment of Dr R T Pidgeon at WAIT in 1981 heralded the introduction of zircon geochronology as yet another geochronological technique available in Western Australia, and there was a corresponding increase in the scientific output of the geochronology group which now comprised geologists and physicists from GSWA, UWA and WAIT. Scientists from the Commonwealth Scientific and Industrial Research Organisation (CSIRO) and industry have also been associated with a number of research projects. A close liaison with geochronologists at ANU has also been a feature of our work. More recently Dr Neal McNaughton was appointed to UWA and he and his students have been actively associated with the laboratory. Together with Ian Fletcher and Kevin Rosman, Neal McNaughton has developed the K-Ca geochronological technique.

In 1979 the Royal Society commissioned a number of reviews describing aspects of science in Western Australia from 1829 to 1979 on the occasion of the 150th Anniversary of the founding of Western Australia. One of these concerned geochronology (De Laeter & Trendall 1979). Figure 2 shows the rate of growth in geochronologically-based publications from 1910 to 1977 taken from that paper.

For the Yilgarn Block

- the time of major generation of gneisses and granitoids was remarkably consistent over almost the entire sampled area of the block, and peaked at about 2700 my;
- there is little evidence for any wide spread about this peak, and evidence for much older ages is still not compelling;
- over a large area of the Block, the granitoids had a relatively short prior-crustal history, and by implication were generated over a relatively brief period;
- the time interval between the formation of the greenstone belts and the peak of granitoid emplacement is of unknown length, but the available evidence suggests that it was small.

For the Pilbara Block

- the main period of gneiss and granitoid generation was also uniform over the area of the Block, and was earlier than that in the Yilgarn Block;
- the error limits attached to granitoid ages make it uncertain whether emplacement was restricted within a narrow time range;
- the highly fractionated small-volume granitoids ("tin granites") are significantly younger;
- greenstone belt ages are about 300-500 Ma older than the peak granitoid age.

Figure 2. Chronological summary up to 1977 of all publications including first reports of ages of Western Australian Precambrian rocks and minerals by methods based on radioactive decay. Selected second reports are also included where these augment or upgrade the first.

In 1981, on the occasion of the 2nd Archaean Conference in Perth, a review of the geochronological data on the two major Archaean terrains of Western Australia was published (De Laeter *et al.* 1981). At that time most of the dates were from Rb-Sr analyses (837 whole-rock and 142 mineral Rb-Sr ages), 137 mineral Pb isotope analyses, and 15 K-Ar analyses, together with some U/Pb data. The judgement was made that, despite the large database, disappointingly few firm conclusions could be enunciated. Nevertheless, the following conclusions were drawn from these data (De Laeter *et al.* 1981):

Zircons are Forever

One of the most intriguing episodes in Western Australian geochronology has been the search for the oldest rocks. In 1981, Denis Gee and his colleagues at the GSWA argued that a predominantly gneissic terrain, which forms an area around the western margin of the Yilgarn Block, was of great antiquity (Gee *et al.* 1981). A study of banded gneisses near Mt Narryer in the northern part of the Western Gneiss Terrain gave a Rb-Sr whole rock isochron age of 3348±43 Ma with an initial $^{87}Sr/^{86}Sr$ ratio of 0.7037 (De Laeter *et al.* 1981). A prior crustal

history of approximately 200 Ma could be inferred, and this was supported by Sm-Nd model ages of 3620 Ma to 3710 Ma from samples of this Meeberrie gneiss (Fig 3). Further work gave a Pb-Pb isochron of 3357 ±70 Ma, whereas Rb-Sr ages for granites intruding the gneisses gave the classic Yilgarn age of approximately 2600 Ma (De Laeter *et al.* 1985). The Sm-Nd ages were interpreted as the time of extraction of the protoliths of the gneisses from a chrondritic source, whilst the Rb-Sr age is thought to represent a time of intracrustal reworking of the gneisses.
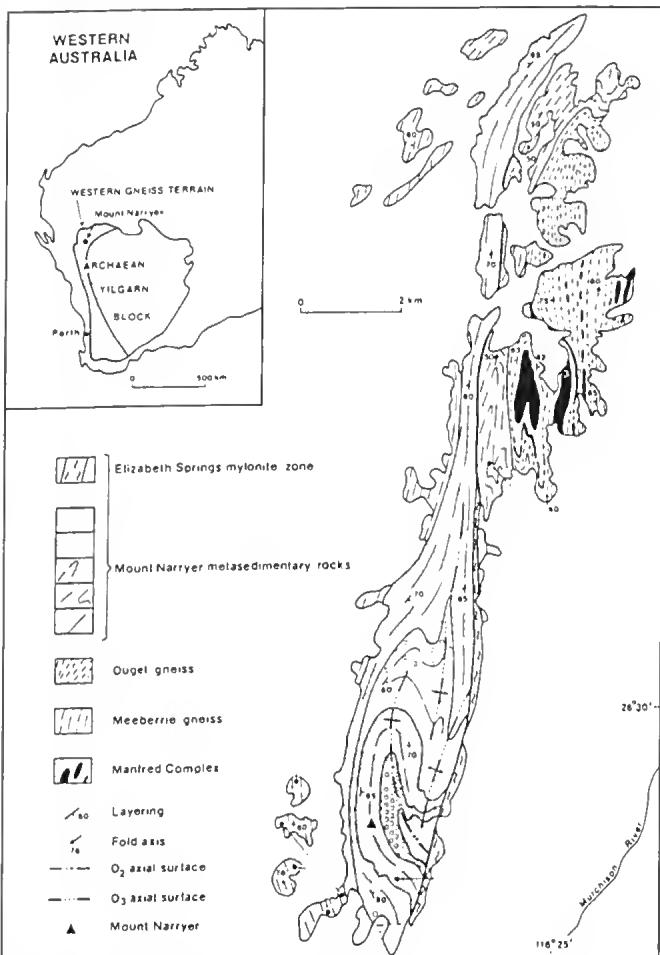
Figure 3. Simplified geological map of the Mt Narryer region, Western Australia.

It was about this time that the **S**ensitive **H**igh **R**esolution **I**on **M**icro **P**robe mass spectrometer (SHRIMP) in the Research School of Earth Sciences at ANU became available for zircon geochronology. Designed by Steve Clement, SHRIMP was the "brainchild" of Bill Compston. After years of development it had already produced some exciting results using the zircon method. However, there was a certain amount of scepticism in various parts of the world as to its real capabilities. Zircons from one of the Meeberrie gneiss samples gave a U-Pb age of 3300 Ma for the rims of the zircons whilst the interior portions gave ages between 3560-3690 Ma (Kinny *et al.* 1988). These older ages have been interpreted as minimum estimates for the original magmatic ages of the xenocrystic cores. These data were in excellent agreement with the conventional geochronology carried out at WAIT, and were convincing evidence of the power of ion probe mass spectrometry.

U-Pb studies by the ion microprobe on detrital zircons from quartzite adjacent to the banded gneiss showed that most of them formed between 3500 and 3750 Ma, although some of them gave ages of about 3300 Ma (Froude *et al.* 1983). These ages suggest that the zircons may have been derived by erosion of the adjacent gneisses or their protoliths. In addition Froude *et al.* (1983) reported the existence of four zircons from the same quartzite which have nearly concordant U-Pb ages between 4100 and 4200 Ma. These results suggest that pre-3800 Ma silica-saturated rocks were present in the Earth's crust. It is possible that intact remnants of these rocks may have survived in this region.

The Jack Hills metasedimentary Belt is a narrow curvilinear east to north-east trending belt approximately 60 km north-east of Mount Narryer. It is composed of minor metabasalts and substantial thicknesses of chert and banded iron formation interleaved with pelitic and psammitic metasediments (Compston & Pidgeon 1986). Detrital zircons from the Jack Hills metasedimentary belt analysed at ANU using the ion microprobe mass spectrometer, has revealed the oldest ages so far determined. One zircon grain registers an age of 4276±6 Ma. which is a minimum estimate for its original age (Compston & Pidgeon 1986). Sixteen other grains have the same or slightly younger age, similar to the zircon ages measured at Mount Narryer. The frequency of occurrence of the old zircons is 12±5%.

Kober *et al.* (1989) report the analyses of thirty zircon crystals from the Jack Hills metaconglomerate using the single zircon, direct evaporation, thermal ionization technique. Four of the thirty zircons gave ages in excess of 4000 Ma, confirming the microprobe analyses of Compston & Pidgeon (1986). Approximately 50% of the analysed zircons yielded an age of 3380±20 Ma, whilst other crystals gave ages of 3300 Ma, 3440 Ma and 3570 Ma. As had been observed at Mount Narryer, some of the zircons demonstrated a more complex age structure with intergrowth of the old phases with younger domains.
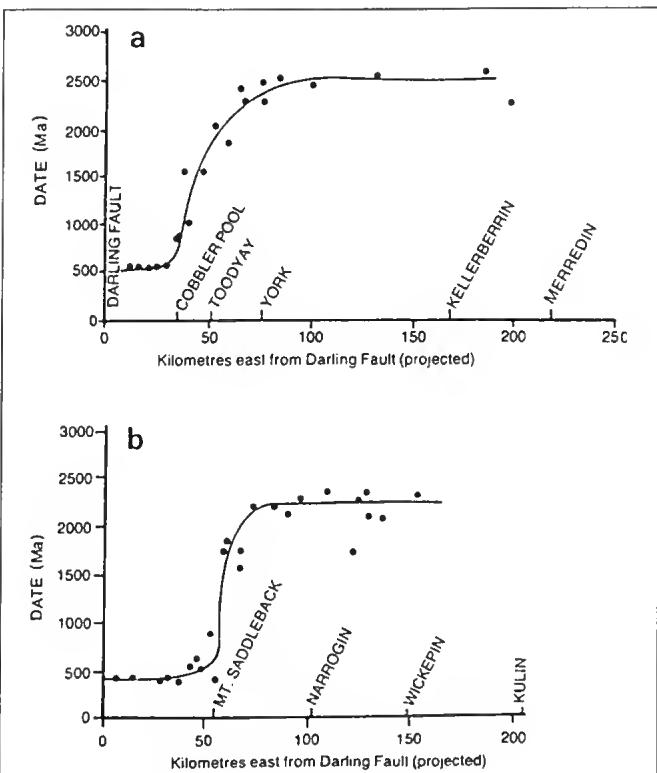
Figure 4. Time-space plots of (a) the Perth and (b) Harvey traverses. Localities have been projected parallel to the western edge of the transition zone, the traverse line being normal to the transition zone.

Although parent rocks with ages in excess of 4000 Ma have not been found, the long-standing belief that Western Australia possesses the Earth's oldest material has been vindicated.

The most recent geochronological publication from the mass spectrometry laboratory at Curtin was in the last issue of the Australian Journal of Earth Sciences (De Laeter & Libby 1993). It describes a profile of Rb-Sr biotite ages from Perth to Kellerberrin and from Harvey to Kulin (Fig 4). The Rb-Sr system for biotites can be reset if the temperature of the rocks exceeds approximately 320C. The ages are between 430-500 Ma in the western most area, then climb quickly through a transition zone, and then are roughly constant at 2300 Ma to the east. We interpret these profiles as representing a period of uplift in the early Palaeozoic.

Cosmochronology

One of the most challenging tasks in nuclear astrophysics is to place a time scale on the events that have occurred in the formation and evolution of the Solar System and on the nucleosynthesis of the chemical elements. Although this is a daunting task, we are aided in our search by the occurrence of a large number of radionuclides, with a wide array of half-lives, that provide the variety of nuclear clocks necessary to achieve this objective. To obtain accurate dating, a decay system should be selected with a half-life that is of the same order as the age of the material to be measured. Thus, long-lived radioactive decay schemes such as U-, Th-Pb, Sm-Nd, Rb-Sr, K-Ar, Re-Os, Lu-Hf and K-Ca have been used to measure the age of events that occurred early in the history of the Solar System, whereas short-lived radionuclides such as ^{10}Be, ^{36}Cl, ^{14}C, ^{3}H, and the U-series disequilibrium system have been used to study more recent events.

Geochronology utilizes isotopic dating techniques to measure the age of terrestrial materials. The radioactivity of certain nuclides also enables them to be used as isotopic tracers of geological processes, such as differentiation sequences in igneous rocks and in the study of mantle-crustal relationships. Isotope geology has now reached a high degree of sophistication, which has only been made possible by the development of sensitive mass spectrometers that are capable of routine measurements of high precision and accuracy. Conventional gas source and solid source mass spectrometers have been successfully applied to the long-lived chronometers, but the short-lived chronometers have required instrumentation with the best possible sensitivity. Ion probe and accelerator mass spectrometers are two such recent developments. Unfortunately the dating of terrestrial materials does not provide a great deal of information on the time of formation of the Solar System, since the Earth is an active planet where a variety of geological processes have combined to destroy the early record of its history.

There are three major epochs in the history of the cosmos. The first epoch T extends from the "Big Bang" to that time when the solar nebula was isolated from galactic nucleosynthesis. The second epoch Δ is of relatively short duration and represents the time interval for the collapse of a gas cloud leading to the formation of the Solar System. The third epoch T_{ss} represents that period from the formation of the Solar System to the present (Figure 5).
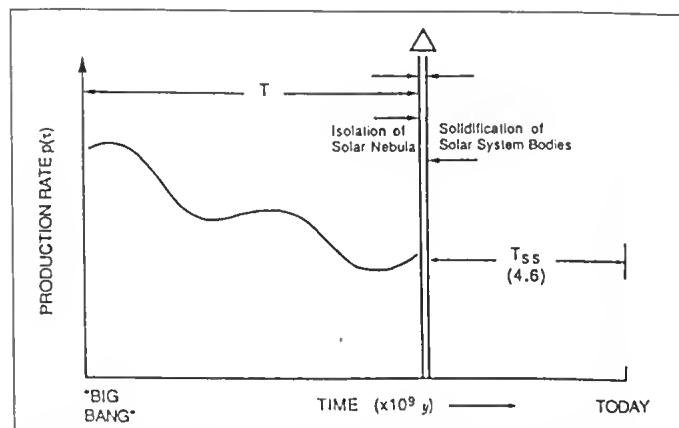
Figure 5. A schematic diagram of the history of the Universe. The first epoch T represents the time period from the "Big Bang" to the isolation of the solar nebula from galactic nucleosynthesis. The second epoch Δ is the time interval between the termination of nucleosynthesis and the solidification of Solar System bodies, while the third epoch T_{ss} represents the age of the Solar System. The shape of the production rate for nucleosynthesis, $p(\tau)$, is for illustrative purposes only.

The Age of the Solar System

Meteorites and lunar samples provide us with alternative avenues to determine the age of the Solar System T_{ss}. Meteorites are the debris of small planetary bodies that solidified early in the history of the Solar System and have been closed isotopic systems retaining evidence of early Solar System processes. Neither have they been subjected to the long planetary accretion processes associated with larger bodies. The first isotopic determination of the age of the Solar System was carried out in 1953 on primordial meteoritic lead (Patterson 1956), resulting in an age of formation for planetary bodies of ~4.5 x 10⁹ years. Exacting chronological studies of a variety of meteoritic materials show that a fine-scale separation of events took place early in the Solar System during planetary formation, and these events may be resolved down to a few million years (Wasserburg 1987).

Numerous chronological investigations of lunar materials were carried out on samples obtained during the various missions to the Moon, from which an excellent chronology has been determined (Wasserburg et al. 1977). Figure 6 shows a representation of lunar chronology. Crystallisation ages of approximately 4.5 x 10⁹ years have been obtained from lunar rocks, so that there is a good correspondence between the meteoritic and lunar data for the time of planetary formation. The melt rocks derived from impact metamorphism give crystallisation ages of (3.85-4.05) x 10⁹ years, and there is good agreement between the U, Th-Pb, Rb-Sr and K-Ar data. This is interpreted as the result of a major bombardment of the moon by meteorites which created the lunar basins. This has been called the "terminal lunar cataclysm", and it is possible that this bombardment affected the Solar System as a whole (Tera et al. 1974). After the termination of the bombardment phase some 3.85 x 10⁹ years ago, there was continued but decreasing volcanic activity until approximately 3.0 x 10⁹ y ago, after which the lunar surface appears quiescent. There is no evidence of recent igneous activity on the moon.
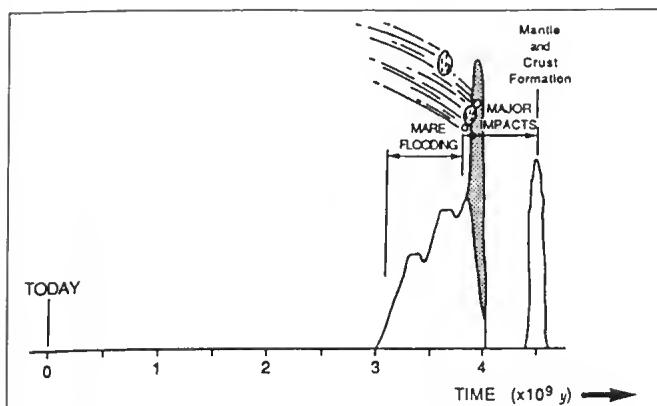
Figure 6. A schematic diagram showing the chronology of major lunar events.

My involvement with the chronology of lunar samples was quite peripheral. In 1971 a fire in a chemical preparation room adjacent to the mass spectrometer laboratory at WAIT badly damaged the mass spectrometer which had been installed in 1968. Although the cost of replacement was covered by insurance, there was a time lag before a new machine could be installed. Fortuitously, Bill Compston was taking up a six month appointment at the Lunar Science Institute in Houston, Texas, and he asked me to supervise his laboratory at ANU during his absence. It was the time of the Apollo missions, and geochronologists were trying to measure the ages of the returned lunar samples. There was intense competition to determine the ages by a variety of techniques, and national as well as personal prestige was at stake.

Bill Compston's ANU laboratory had reported Apollo 14 Rb-Sr ages which were systematically greater by a few percent than other reported measurements. Compston was to present a paper at the Lunar Conference which would attempt to justify the ANU results. However, there was a possibility that the elemental Rb/Sr ratios measured at ANU on the lunar samples were wrong, because of systematic errors in the calibrations of the Rb and Sr isotopic spikes. The US National Bureau of Standards had just produced some certified stoichiometric Rb Cl (SRM 984) and Sr CO_3 (SRM 987) standards and it was decided to recalibrate the ANU spike solutions against these new standards. Working around the clock, we managed to complete the work just before the Lunar Science lecture where Bill Compston was able to announce a 1.8% error in the calibrations which necessitated a decrease in all the previous ANU ages for the Apollo samples. The revised ages were then in good agreement with Wasserburg's group at Cal Tech (De Laeter *et al.* 1973). I also worked on the Apollo 15 lunar samples at ANU before returning to Perth in mid 1972 (Compston *et al.* 1972).

Extinct Radionuclides

A number of unsuccessful mass spectrometric attempts were made to demonstrate the existence of short-lived radionuclides early in the evolution of the Solar System before John Reynolds showed that a large enrichment of ^{129}Xe existed in Xe extracted from the Richardton meteorite (Reynolds 1960). In 1961 Peter Jeffery and Reynolds proved that the excess ^{129}Xe was correlated with iodine in the

meteorite, thus proving that the decay of the radionuclide ^{129}I (whose half-life is 17×10^6), had taken place within the meteorite itself (Jeffery & Reynolds 1961). It was possible to calculate a time $\Delta \sim 10^8$ years between the synthesis of ^{129}I and the formation of the Solar System. The value of $\Delta \sim 10^8$ years created somewhat of a dilemma, because astrophysical models predicted a much shorter time interval for the formation of the Solar System.

One reason behind the search for evidence of extinct radionuclides in meteorites was to identify the heat source that melted some of the meteorite parent bodies. One of the most logical candidates was ^{26}Al, which decays to ^{26}Mg with a half-life of 0.72×10^6 years. I was associated with the first mass spectrometric study to identify the presence of this potential heat source by the measurement of the isotopic composition of Mg in meteoritic feldspars whilst I was at McMaster University in 1967 (Clarke *et al.* 1970). Although this initial attempt was unsuccessful, a study of calcium-aluminium rich inclusions from the Allende meteorite by Chris Gray and Bill Compston gave an excess in ^{26}Mg, which was shown to be correlated with Al, in an isochron-type array (Gray & Compston 1974). Figure 7 shows an ^{26}Al/^{26}Mg isochron from Lee *et al.* (1977). A plausible interpretation is that ^{26}Al was present in the meteorite and that the decay was *in-situ*. If it is assumed that the minerals were isotopically homogeneous at the time of solidification, a value of Δ of $\sim 10^6$ years can be calculated. This is significantly lower than the value of $\sim 10^8$ years derived from ^{129}I-^{129}Xe systematics, and much closer to astrophysical estimates.
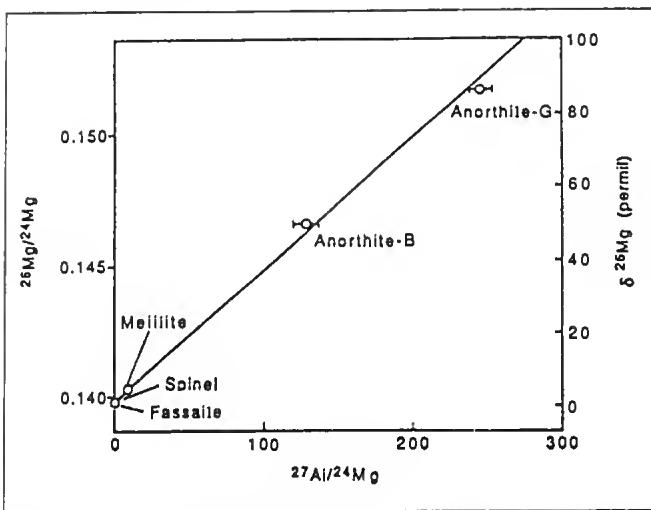
Figure 7. An "isochron" diagram of ^{26}Mg/^{24}Mg versus ^{27}Al/^{24}Mg for minerals from an Allende inclusion. The linear dependence of the magnitude of the anomalous ^{26}Mg on the Al/Mg ratio can be interpreted as resulting from the decay of the radioactive nuclide ^{26}Al.

Another extinct radioactive system is based on the decay of ^{107}Pd (with a half-life of 6.5×10^6 a) to ^{107}Ag. Kelly & Wasserburg (1978) proved the existence of excess ^{107}Ag in iron meteorites with ^{107}Ag excesses of up to 20%. The excess ^{107}Ag correlates with Pd to form an "isochron" with a calculated Δ of $\sim 10^7$ years between the last injection of nucleosynthetic material and the melting and differentiation of small planetary bodies. A ^{135}Ba enrichment, which was observed in an Allende inclusion by McCulloch & Wasserburg (1978b), is due to the decay of ^{135}Cs (which has a half-life of 3.3×10^6).

A number of other extinct radionuclides may be present in meteoritic material. Kevin Rosman and I investigated the decay of ^{126}Sn to ^{126}Te (with a half life of 10^5) in iron meteorites, but could find no evidence of excess ^{126}Te. This provides a lower limit of 10^6 years for Δ (De Laeter & Rosman 1984).

The study of extinct radionuclides therefore provides the following scenario: interstellar material, containing a full range of nucleosynthetic products (including some radionuclides that are now extinct), condensed to form a molecular cloud in a time period of 10^8 years (as estimated from the ^{129}I/^{129}Xe chronometer). Rapidly evolving stars provided a "last minute" injection of fresh nucleosynthetic material, including ^{26}Al and ^{107}Pd, into the condensing cloud from which the Solar System was formed within a time period of a few million years.

Nucleocosmochronology

Nucleocosmochronology is the use of the relative abundances of radioactive nuclides to determine the time scales for nucleosynthesis of these nuclides. Schramm & Wasserburg (1970) showed that a nucleosynthetic formalism can be developed for long-lived radionuclides, and that this can give the mean age of the elements, independent of the time-dependent production model adopted. This mean age is a lower limit to the period T over which nucleosynthesis has taken place.

The estimate of the duration of nucleosynthesis is a challenging scientific problem. If we can calculate this period T, then we can estimate the age of the galaxy T_G by adding T to the age of the Solar System T_{ss} and the formation age of the Solar System Δ, such that

$$T_G = T + \Delta + T_{ss.}$$

This estimate is then a lower limit for the age of the universe.

I have already mentioned the work on the ^{176}Lu/^{176}Hf cosmochronometer by Malcolm McCulloch, Kevin Rosman and myself in the mid-1970s, (McCulloch et al. 1976). I was anxious to calibrate this chronometer because I thought it offered the best chance of measuring the duration of nucleosynthesis and hence the age of the Universe.

Although the ^{176}Lu/^{176}Hf ratio was known from mass spectrometric determinations in our laboratory, and the neutron capture values and half life of ^{176}Lu had been measured, the nuclear systematics of ^{176}Lu were not well understood in the mid 1970's. When ^{176}Lu is formed by the capture of ^{175}Lu by a neutron, it can exist in two isomeric states - the ground state which decays to ^{176}Hf with a half life of 3.57×10^{10}a, and an excited state which has a half life of only 3.68 hours (Figure 8).

In the mid 1970's it was believed that the two states were completely independent and thus all that was required was to measure the branching ratio B, that is find out what fraction of ^{176}Lu existed in the ground state. I persuaded some nuclear physicists at Lucas Heights Atomic Energy Establishment in NSW to help me to measure the branching ratio in their nuclear accelerator, which could simulate the
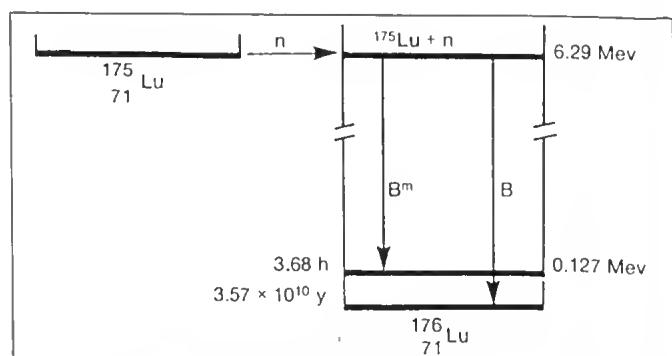
Figure 8. Decay scheme for neutron capture on ^{175}Lu, showing the two possible radioactive decay modes of ^{176}Lu to ^{176}Hf.

conditions that existed in red giant stars. We obtained a value of B = 21% (Allen et al. 1981). I remember, as if it was yesterday, making the calculations to estimate the age of nucleosynthesis from the data, and the shock of finding a negative age. This implied that the Big Bang had not yet occurred! There was obviously a small problem somewhere. So for the next 12 months or so, we laboriously repeated the branching ratio experiment, necessitating several trips to Lucas Heights. However, the value remained essentially unchanged. Furthermore our value was in conflict with a value of B from a much more prestigious group in Karlsruhe in Germany (Beer et al. 1984), so that we were understandably nervous about our conclusion, which was that the ^{176}Lu/^{176}Hf chronometer couldn't keep time.

The correct answer finally emerged when the energy levels of ^{176}Lu were remeasured. It turned out that the energy separation between the ground state and excited state of ^{176}Lu was much smaller than first reported in the literature, and at the temperatures which existed in red giant stars (10^8 K), the two states could overlap and hence the ^{176}Lu ground state could leak away via the ^{176}Lu excited state to ^{176}Hf. This problem is somewhat akin to the U-He leakage method. ^{176}Lu was a cosmothermometer not a cosmochronometer (De Laeter et al. 1988). Sufficient to say that this was a terribly disappointing result. I had spent almost ten years of research investigating the age of the Universe only to find that Nature had managed to frustrate us. The one pleasing fact that has emerged is that our conclusions have now been accepted by the international scientific community, including the Karlsruhe group (Lesko et al. 1991).

An independent estimate of the age of the Universe, calculated from the Hubble recession of the Galaxies, is approximately 19×10^9y (Sandage & Tamman 1982). Other astrophysical evidence on globular clusters, and estimates of the age of nucleosynthesis by the U-Pb (Thielemann et al. 1983) and Re-Os (Yokoi et al. 1983) cosmochronometers, give tentative support to this value, but it must be emphasised that the age is an approximate value with large uncertainties.

Thus cosmochronological studies have provided a reasonable time scale for the early history of the Solar System, including the age of formation of the meteorites. Some success has also been achieved in deriving a mean age of galactic nucleosynthesis, but the age of the galaxy has not yet been accurately determined from nucleocosmochronological studies due to the constraints associated with each of the long-lived chronometers used to determine the duration of nucleosynthesis.

Conclusions

I have endeavoured to give you a cursory glimpse of our endeavours to delve into that most intriguing Question of Time. As Arthur Holmes' has said:

"It is perhaps a little indelicate to ask our Mother Earth her age, but Science acknowledges no shame, and from time to time has boldly attempted to wrest from her a secret which is proverbially well guarded".

My journey in time commenced in 1968 when Alec Trendall and Bill Compston came to visit me in the Mass Spectrometry Laboratory at WAIT 25 years ago, almost to the day, and persuaded me to assist in that indelicate question of asking Mother Earth her age.

Looking back down that 25 year time period (which is something I probably wouldn't have done if it was not for this Lecture) my over-riding impression is how much still remains to be achieved. Although we have developed beautiful "high-tech" mass spectrometers and many measurements have been made, some of the objectives we set out to achieve haven't been accomplished. But I look to the future with confidence. SHRIMP is a mass spectrometer which is ideally suited to unravelling the problems of mineral exploration, and we have an excellent team of physicists and geologists from UWA, GSWA, and Curtin together with overseas collaborators, who can exploit its potential to the full.

My most enduring memories of my chronological odyssey have been the people I have worked with, the friendships made, the teamwork forged, the localities visited. Maybe one day we will learn all the answers, but in the meantime perhaps we should listen to Tolly Cobbold's injunction "Time, Gentlemen, Time", and leave some of the questions to another time and perhaps to another Royal Society Medallist to answer.

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The Impact of Prolonged Flooding on the Vegetation of Coomalbidgup Swamp, Western Australia.

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Abstract

A preliminary study of the impacts of prolonged flooding on the vegetation of Coomalbidgup Swamp, an ephemeral wetland near Esperance, Western Australia, identified changes in composition and physiognomy of dryland and wetland vegetation. A high mortality was observed after flooding for all species typically part of the surrounding dryland flora. Some stands of wetland and dryland vegetation have been partially inundated for up to 6 years, which has resulted in 100% mortality of dryland species. The wetland species, *Melaleuca cuticularis* and *Eucalyptus occidentalis*, showed tolerance towards these conditions, although 45.5% of the individuals that were healthy prior to flooding were either dead or dying after prolonged flooding. There was no apparent relationship between tree vigour and age.

Melaleuca cuticularis and *Eucalyptus occidentalis* seedlings emerged around the wetland margins within months of the water levels receding. Little recruitment of native dryland species was evident even 2 years after water had receded. However, extensive weed invasion and establishment of *E. occidentalis* and *M. cuticularis* in this zone contributed to a change in composition of the peripheral vegetation. Secondary salinity and the extent of flooding within the catchment is likely to increase, leading to further degradation and change in wetland vegetation. The study provides an insight into the possible effects of altering the flooding regime of ephemeral wetlands.

Introduction

The species composition of wetland vegetation is influenced primarily by water regime, the key parameters being water depth, flooding frequency and duration. Flooding tolerance varies depending on species, age and quality of floodwaters, however rhizosphere oxygen deprivation is eventually fatal to all species irrespective of their flooding tolerance. Even among wetland species, there are no known cases of any prolonged survival over weeks or months of roots being entirely deprived of oxygen (Crawford 1992). Death of wetland plants, as a consequence of prolonged flooding, accelerates wetland degradation because of a reduced or ineffective buffer to nutrient input, reduced evapotranspiration resulting in increased capillary rise of saline water, destabilisation of sediment, and loss of food source and habitat for fauna.

Changes in water regime and water quality that lead to the decline of wetland vegetation are usually associated with disturbances within the catchment but are external to the wetland (Froend *et al.* 1987; Froend & McComb 1991). Removal of native dryland vegetation results in increased groundwater recharge, associated increased mobility of salt stored in sub-soils, and increased salt and nutrient concentration in the wetland. There have been few south-western Australian studies which have examined the process of wetland vegetation degradation due to salinity and waterlogging, and/or nutrient enrichment, although degradation is widespread in the south-west (Halse 1993). Of the Western Australian rural wetlands studied to-date,

e.g. Lake Toolibin (Mattiske 1978; Froend *et al.* 1987; Halse 1987; Anon. 1987; Bell & Froend 1990) and Lake Towerrinning (Froend & McComb 1991), the development of secondary salinity and waterlogging within the catchment has been well advanced by the time of study. Little is known about the changes that wetland plant communities undergo during the early part of the process of secondary salinisation and waterlogging. Without baseline data collected before or during the early phases of vegetation change, it is difficult to understand the ecological processes involved. At present we rely largely on historical information to determine the sequence of events which lead to environmental change and degradation.

Of particular importance is the impact that increased salinity and waterlogging has on the recruitment of wetland plants. Most species are dependent on seed production, germination and seedling establishment for successful recruitment, although sedges, rushes and submerged macrophytes readily reproduce by vegetative means (Froend *et al.* 1993). If increased salinity and waterlogging results in the death or degradation of mature individuals at lower elevations, then the continued survival of the population is dependent on the successful recruitment of seedlings at higher elevations. The effect of salinity and waterlogging on germination at higher elevations in the species range at a wetland is therefore critical.

On the south coast of Western Australia near Esperance, a combination of extensive clearing and above-average rainfall years (1986, 1989) caused increased groundwater recharge and surface water retention to an extent where natural ephemeral water courses and basins have retained

surface water for prolonged periods. One ephemeral wetland, Coomalbidgup Swamp, has reportedly contained surface water since the winter of 1986. During 1989, winter rainfall in the catchment was heavy, causing severe water erosion and flooding in the catchment (Anon. 1990), and increased water levels in the swamp. Mortality of fringing wetland and dryland vegetation has resulted due to prolonged inundation.

Coomalbidgup Swamp provides an opportunity to examine changes in wetland vegetation structure and composition as a consequence of unusually high water levels and a prolonged flooding period. As the catchment had been cleared in relatively recent times (since 1964), the study permitted the examination of wetland plant community response at a relatively early phase of altered catchment history (cf. wheatbelt catchments). The aspects of wetland vegetation dynamics that were investigated include the extent of vegetation mortality as a result of the 1986 and 1989 flood events, the success of seedling recruitment, and the colonisation of the swamp banks as water levels receded.

Study Area

Coomalbidgup Swamp is situated approximately 45 km west of Esperance, Western Australia. A single intermittently-flowing creek drains an area of 97 km^2 and empties into the swamp from the north-east (Fig 1). Most of the Coomalbidgup catchment (approx. 95%) was cleared for agriculture during 1964-1972. Small areas of remnant vegetation exist primarily along water courses and around wetland basins, and the vegetation surrounding Coomalbidgup swamp represents the largest stand of native vegetation in the catchment. Secondary salinity is not currently a major concern within the catchment, however, research by the Western Australian Department of Agriculture (Bob Nulsen, *pers. comm.*) indicates that subsoil salt stores in the catchment are extensive, and pronounced salinisation will occur in the near future with continued elevation of groundwater levels.
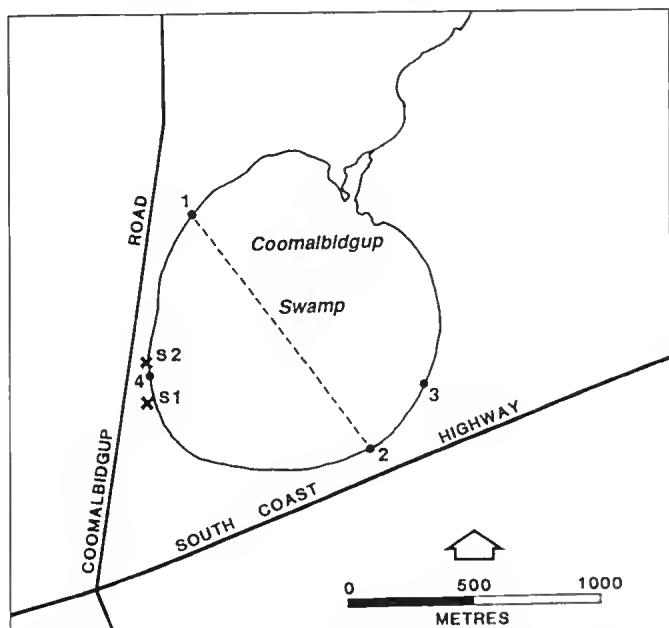
Figure 1. Location of sample sites at Coomalbidgup Swamp. Sites 1, 2, 3 and 4 represent the shore transects, and S1 and S2 the seedling plots. The traverse transect is shown by the dotted line between shore transect 1 and 2.

The area has a 25 year average (1965-89) annual rainfall of 480 mm. The annual rainfall during 1989 was 35% above the average, and contained the wettest two, three, and four consecutive months recorded since 1969. Runoff in the catchment of Coomalbidgup Swamp is generated after several months of high rainfall rather than by a single wet month or individual high intensity storms of shorter duration. As the water table rises and saturated areas within the catchment increase, an increased proportion of rainfall is expected to runoff. As a result, there is increasing pressure to implement water management programs on agricultural land within the catchment (Anon. 1990). Diversion of excess water into natural water courses downstream, via a system of contour banks and drains, is one means used to control salinity and waterlogging. Wetlands therefore, are receiving much more water and salt than under natural conditions.

Methods

Species Distribution and Mortality - Transects

Permanent belt transects were established at 4 sites around Coomalbidgup swamp in June 1990 (Fig 1) to represent the different plant communities present. Each transect was 30m x 2m with one end at the water's edge; both ends were marked with a star picket. Changes in elevation along the transects were determined at 2m intervals using a dumpy level. For comparison between swamp and terrestrial vegetation, each transect was extended 50 - 60m into the lake to include inundated trees and shrubs on the swamp bed. Due to the depth of water, the identity of dead understorey species on the deepest part of the transect could not be recorded.

Vegetation physiognomy, species presence and mortality were recorded at 2m intervals along the transects during June 1990 and June 1992. Sampling in June 1990 took place sufficiently close to the time of death to determine the identity of most species. Specimens were collected of all species and identified at the Western Australian Herbarium.

Species Distribution, Vigour and Mortality - Traverse

A permanent transect traversing the swamp was established between transects 1 and 2 in June 1990 (Fig 1). A compass bearing of 145° (from transect 1) was followed by boat and each tree that occurred within 1m either side of the boat was tagged, species recorded, trunk diameter at the height of the tag (1 m above 1990 water level) and tree height measured and vigour determined. Water depth was recorded at approximately 20m intervals or at major changes in tree composition/distribution. Understorey species were not recorded due to the water depth. The traverse was re-visited during June 1992 and the vigour of all tagged trees determined.

Vigour was estimated using a scale of 1 to 5; 1 = dead for >1 year, no leaves; 2 = many dead/dying branches, few green leaves visible; 3 = visible signs of stress but 50 - 70% green canopy ; 4 = visibly healthy with few signs of stress, 70 - 90% green canopy ; 5 = healthy, no signs of stress, 90 - 100% green canopy. A vigour class of 1.5 was assigned to trees which appeared to have died recently (within the last year), judging by the persistence of dead leaves. Height was determined with an extendable tree measuring pole. Trunk diameter at tag height was measured with a diameter tape.

Seedling Plots

Two seedling plots were established in June 1990 to determine the density of seedling recruitment on the banks of the swamp. Both plots (S1 and S2; Fig 1) were situated close to the swamp shore and orientated perpendicular to the shoreline. The size of the seedling transects varied according to the density and distribution of seedlings; S1 was 15 x 10m and S2 was 10 x 6m. The sites chosen for the transects were representative of recruitment observed in open shrubland (S1) and closed woodland (S2). Recruitment only occurred along the flotsam line(s) on the shore. Each plot was divided into 1m² cells within which the density and maximum height of each seedling species was determined.

Results

Transects

The species present and their distribution at each of the transects is shown in Fig 2a - d. Transect 1 vegetation at June 1990 varied from *Banksia speciosa* low (4-5m) woodland on the upper and lower slopes of the present shore, to *Eucalyptus occidentalis* tall (12-14m) woodland on the lake bed (Fig 2a). Understorey growth on the shore was dense, the dominant species being *Jacksonia spinosa*. Apart from a few deaths of *J. spinosa*, more likely due to insect attack or 'natural' senescence, there were no apparent deaths due to flooding on the upper slope of the shore. The lower part of the shore and the nearshore shallows displayed a high mortality of species present before flooding, though *Amphipogon* sp. and *Patersonia occidentalis* were relatively tolerant, and the introduced species *Cirsium vulgare* and *Solanum nigrum* invaded the saturated soils. The presence of *E. occidentalis* seedlings near the June 1990 shoreline, suggests a transition from scattered wetland vegetation on the swamp bed to a littoral community. The presence of dead *B. speciosa* in the nearshore shallow water indicated that the dryland sandplain vegetation once extended below the June 1990 shoreline. On the lake bed itself *E. occidentalis* was the only species observed.

The June 1992 water level was approximately 2 metres lower than in June 1990. Due to the death of the original trees and shrubs and the moist sediment, the area submerged during 1990 but exposed in 1992 represented ideal ground for weed invasion and recruitment of wetland species. As a result, a significant increase in the density of weed and herbaceous native species was recorded on the exposed sediment in June 1992. Species such as *C. vulgare, Hypochaeris glabra, Sonchus oleraceus* and *Eragrostis curvula* were prevalent on the damp exposed shoreline. There was also extensive recruitment of *E. occidentalis* and *Melaleuca cuticularis* seedlings between 1990 and 1992 as the water level receded.

The shore vegetation of Transect 2 (Fig 2b) was typified by a mid-high (0.5-1m) shrubland with emergent *E. occidentalis* and *M. cuticularis* trees. Although there was no structurally dominant species in the understorey, common species were *Grevillea nudiflora, Leucopogon spp.* and *Hibbertia hypericoides*. The slope of the shore at Transect 2 was shallower than that of Transect 1 indicating wetter conditions over a greater area of the transect. This is supported by the presence of *M. cuticularis* on the mid to lower slopes of the shore. Vegetation on the lake bed consisted of *M. cuticularis* mid-high woodland, with dead *Beaufortia* sp., *Acacia alata* and *Hakea laurina* closer to the shore. Shrubs common on the upper slopes of the shore

(e.g. *Micromyrtus elobata* and *G. nudiflora*) showed a high degree of mortality when present on the lower flooded areas. Live plants of the lower shore and near shore areas were typically those tolerant of waterlogged conditions, such as *E. occidentalis* and *M. cuticularis*; the introduced species *S. nigrum* also invaded the saturated sediment. The pattern of tree deaths on the lake bed was similar to those of Transect 1. From these remnants of dead vegetation in the nearshore region, it is evident that the dryland vegetation extended 20-30m further downslope of the June 1990 water level. Transect 2 in June 1992, like Transect 1, displayed extensive weed (*C. vulgare, S. oleraceus, Rumex acetosella*) establishment in the area that was submerged in 1990. Both *E. occidentalis* and *M. cuticularis* seedlings had also established over most of this area.

The vegetation of Transect 3 (Fig 2c) was similar in structure and dominant species composition to Transect 1. A *B. speciosa* low (3-6m) open woodland covered the shore and a *E. occidentalis* tall woodland covered the lake bed. Dominant shore species were *Leptospermum erubescens* and *Melaleuca thymoides*. There was high mortality amongst all the species in waterlogged and flooded parts of the transect except seedlings of *E. occidentalis* and *M. cuticularis*, and the introduced species *C. vulgare* and *S. nigrum* which probably established soon after water levels began to recede. The sandplain vegetation had extended 20-30m further downslope of the June 1990 water level. The mortality amongst the *E. occidentalis* on the lake bed was similar to the other transects. Transect 3 in June 1992, like all other transects, had extensive weed (*C. vulgare, S. oleraceus, E. curvula*) and native herb (*Senecio quadridentatus, Epilobium billardierianum, Dampiera sericantha, Muehlenbeckia adpressa, Juncus pallidus, Velleia trinervis*) establishment in the area that was submerged in 1990. Both *E. occidentalis* and *M. cuticularis* seedlings had also established over this area.

Vegetation on Transect 4 (Fig 2d) was similar in structure to Transect 2, with the understorey being mid-high shrubland covered by scattered emergent *E. occidentalis* and *M. cuticularis*. However, the dominant shrubs of the understorey (*Hakea corymbosa, Phymatocarpus maxwellii* and *A. sulcata*) were different to those of Transect 2. Emergent *E. tetragona* and the shrubs *Acacia subcaerulea, Hibbertia acerosa* and *Melaleuca striata* were only found at the uppermost, and driest, part of the transect. The pattern of shrub and tree deaths was also similar to Transect 2. Transect 4 in June 1992 had weed (*C. vulgare*) and native herb (*S. quadridentatus, E. billardierianum, D. sericantha, V. trinervis, E. monostachya*) establishment in the area that was submerged in 1990. Both *E. occidentalis* and *M. cuticularis* seedlings also established over most of this area.

At all the transects, small seedlings of *E. occidentalis* and/or *M. cuticularis* were found within 2-6m of the shore in June 1990 and 1-26 m of the shore in June 1992. These seedlings were of varying age and had germinated between winter 1989 and autumn 1992. Generally the age of the seedlings increased with increasing elevation.

Traverse

The lake is a flat-bottomed basin with gently sloping sides and had a maximum depth of approximately 5m during the 1990 sampling period.
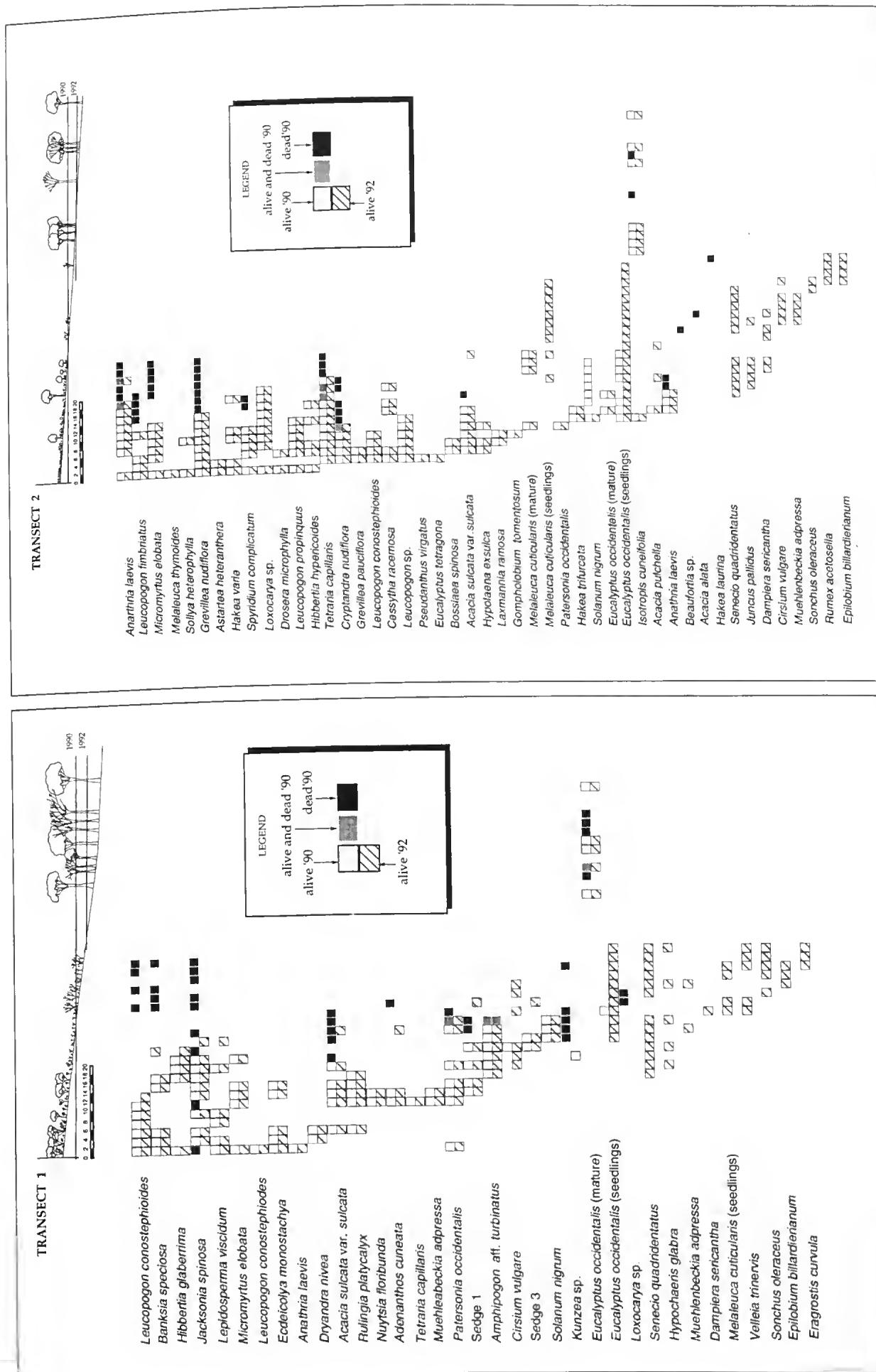
Figure 2. Profile diagrams and species distribution along shore transects 1-4. Height and distance are to scale.
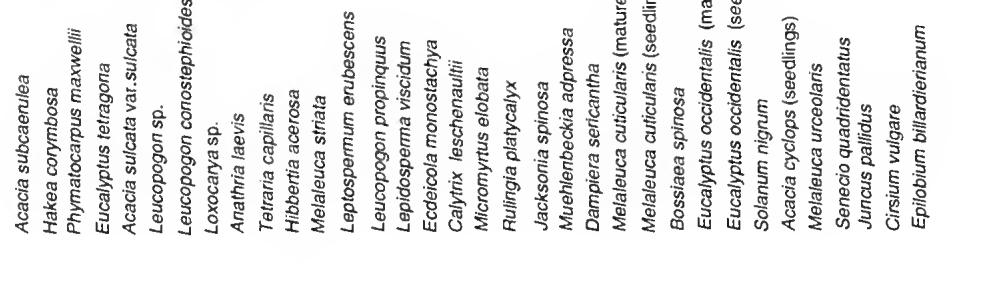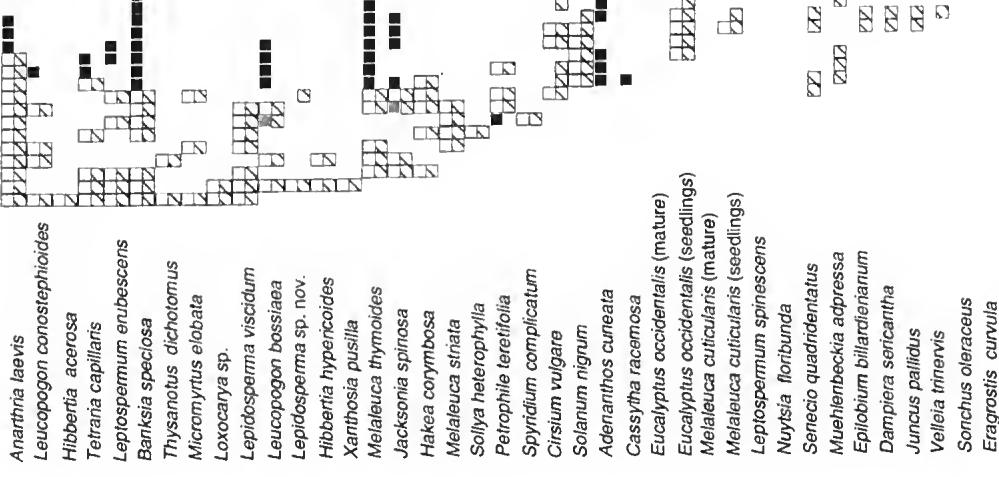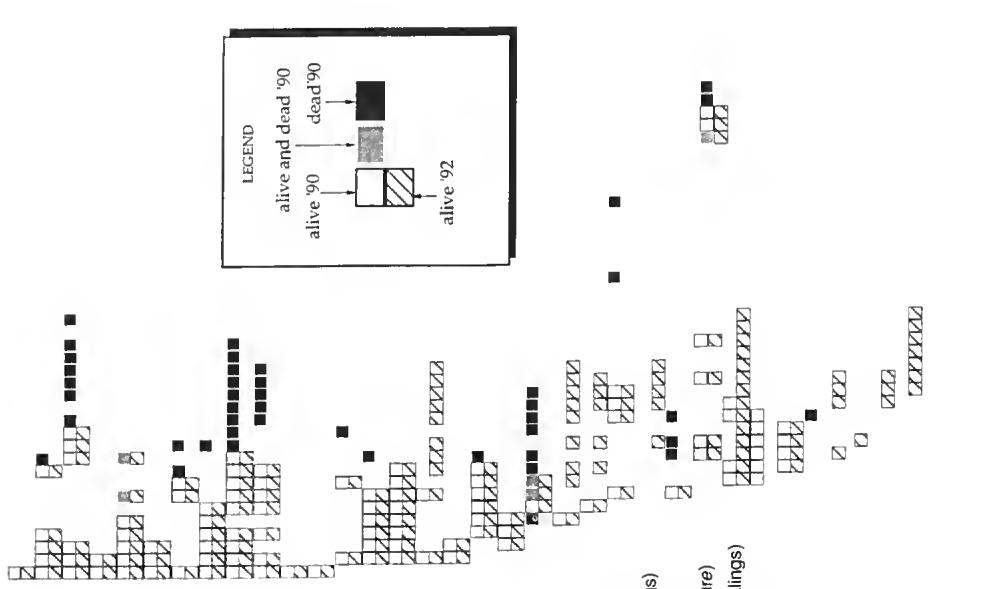
Figure 2.—*continued*

Table 1 shows the vigour classes of the trees sampled and the mean trunk diameter of each class. A total of 173 *E. occidentalis* and 18 *M. cuticularis* plants were recorded along the 1100m transect. It was noted that tree deaths (*E. occidentalis*) along the transect could be classified into two groups, those that had recently died (≤ 1 year ago), and those which had been dead for a much longer period of time. The latter group consisted of 107 (61.8%) trees which perished in a fire in December 1976 (neighbouring landowners, *pers. comm.*). This was evident in the lack of bark and minor branches, weathered trunk and absence of dead attached leaves. Even though local residents report that the lake has not dried since the 1986 flood event, post-1976 tree deaths were very recent (≤ 1 year before sampling). This implies that the inundation between 1986 and 1989 was not sufficient to cause tree death within that period, and that the recent mortality observed on the lake bed is a response to the cumulative effect of the significantly higher water levels after the 1989 flood event. Mortality of the dryland vegetation is also likely to be due to the 1989 flood, as there is no evidence to suggest this vegetation was inundated after the 1986 flood. All recent deaths and poor vigour of the lake bed trees were assumed to be due to prolonged inundation since 1986. Of the remaining live trees most were found to be in poor to fair health (vigour class 3 & 4). In June 1990, trees that had died or were dying since flooding (vigour classes 1.5 and 2) comprised 21.2% of trees alive prior to flooding (Table 1). The June 1992 monitoring of the trees showed that the proportion of dead and dying trees increased to 45.5% of those trees alive prior to flooding. Most live trees remained in the poor to fair health categories, however, there was an increase in the number of dying trees (from 5 to 9) and poor health trees (15 to 24). There was a decrease in the number of fair health trees (from 31 to 12) and healthy trees (from 6 to 0), and the number of live trees (classes 2, 3, 4 and 5) decreased from 55 (83.3%) to 45 (68.2%).

Apart from an area of small diameter trees in the last 250m of the traverse (SE end), there was no apparent pattern of distribution of vigour and diameter classes, and height across the transect. Figure 3 shows the trunk diameter classes versus vigour categories for the trees on the traverse.

Most trees sampled were of small to medium diameter, 0 - 16 cm. However, the numbers in these classes were made up significantly by trees that perished in the 1976 fire (Dead category = vigour class 1; Fig 3). This indicates that at the time of the fire a large proportion of the population died, and the survivors have matured since, increasing the range in diameter classes. Trees that had recently died or were dying as a result of prolonged flooding (Recently Dead category = vigour class 1.5 + 2), were mostly medium to large in diameter (up to 26-28 cm) but with a significant number of small diameter trees. Live category trees (vigour class 3+4+5) had the widest range of diameter classes from 2 cm to 36 cm, with most less than 22 cm.
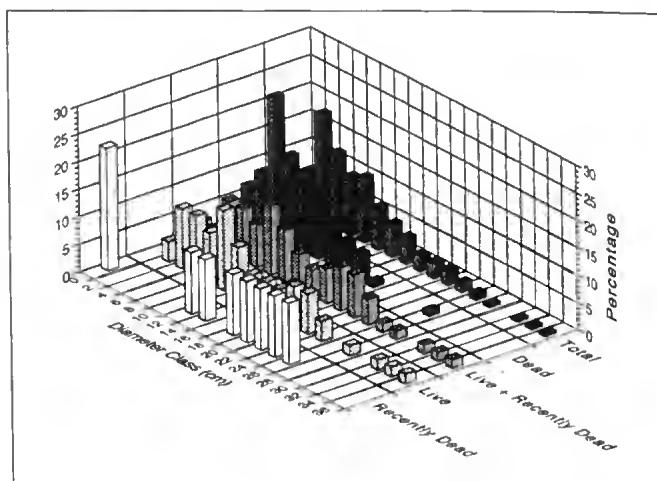
Figure 3. Proportion of trees in each trunk diameter class for different vigour categories. Vigour category Dead = vigour class 1; Live and Recently Dead = vigour class 1.5+2+3+4+5; Live = vigour class 2+3+4+5; Recently dead = 1.5+2. See methods for definition of vigour class.

Seedling Plots

Seedlings were found amongst the flotsam (dead leaves, capsules, seeds) that collected in a series of lines along the shore of the swamp. It is suggested that the trees on the lake bed may have flowered and dropped seed on the water

Table 1

Number (N) and percentage of total trees in each vigour class, and trunk diameter (mean, standard error and range) of trees sampled along the traverse (see Fig 1) for 1990 and 1992

| | 1990 | | 1992 | | 1990 TRUNK DIAMETER (cm) | | |
VIGOUR CLASS	N	% total	N	% total	MEAN	S.E.	RANGE
ALL CLASSES	173		173		10.43	0.54	1-36
1 (Dead)	107*	61.8	125	72.3	7.93	0.45	1-26.8
1.5 (Recently Dead)	9	5.2	3	1.7	16.22	3.25	1-26
2 (Dying-very Poor Health)	5	2.9	9	5.2	6.68	1.50	3.1-13
3 (Poor Health)	15	8.7	24	13.9	13.19	1.90	5.4-28.5
4 (Fair Health)	31	17.9	12	6.9	16.55	1.37	5.9-34
5 (Healthy)	6	3.5	0	0	14.92	5.87	4.8-36
Number of trees alive prior to flooding	66						
Number of Recently Dead+Dying Trees	14		30				
(% of trees alive prior to flooding)	(21.2)		(45.5)				

*trees died during 1976 fire prior to flooding

surface each year since the 1989 flood. Measurements of seedling density in June 1990 show variation in seedling numbers in relation to the distance from the water's edge, with peak density at the flotsam lines (Fig 4). At the time of sampling, seedling height on the upper flotsam line (Plot 1) was up to 30 cm, and less than 5 cm on the lower flotsam line would have germinated in Autumn 1990 (just prior to the June 1990 sample date). Only a small proportion of the seedlings observed were *M. cuticularis* (Plot 1 only). This is probably due to the relative scarcity of this species at the swamp combined with the timing of seed release. The higher

seedling density in Plot 1 may be due to the very open tree and shrub canopy and presence of larger areas of bare ground. At Plot 2, where seedling density was lower, the tree and shrub canopy was dense, therefore restricting light, and the ground was covered with a deep litter layer. Although the seedling plots were not monitored in 1992, it was noted that further flotsam lines developed at lower elevations as the water level receded. This resulted in up to 4 lines (1989-92) of seedling recruitment decreasing in age from high elevations to lower elevations. However these lines were not pronounced where dense vegetation/debris broke up the flotsam. Although not measured, a significant increase in *M. cuticularis* seedlings on the swamp shore was noted in June 1992.

Discussion

The results of this study document the detrimental effect of abnormally high lake levels and prolonged flooding. In all four transects, a high mortality was observed for all species typical of the surrounding dryland sandplain flora. The duration and depth of flooding that resulted in plant mortality is difficult to determine. Local farmers recall that the swamp "filled" during heavy rains of 1986 and has not dried, or had substatial lowering of water levels, since. If this is the case, then plants at lower elevations on the shore transects would have been partially inundated or submerged for up to 4 years by 1990 and 6 years by 1992. However, the evidence suggests that plant mortality at higher elevations on the shore transects occurred ≤ 1 year before June 1990. Those plants at lower elevations on the shore transects (*i.e.* totally submerged in 1990) may have died relatively soon after inundation in late 1986 or 1987. The water depths where dead plants were found in June 1990 varied from waterlogged (up to 50 cm upslope of the June 1990 level) to 3m depth.

As a consequence of the deaths of dryland species, the width of the remaining peripheral dryland vegetation at some parts of the swamp was reduced by one half. Such vegetation is vital to the conservation of wetlands because it acts as a buffer to disturbance and runoff, and is often the only intact native vegetation and habitat for fauna in agricultural areas.

More than 45% of the trees on the lake bed that were alive at the time of the 1989 flooding were either dead or dying by 1992 as a result of prolonged flooding. Mortality of the lake bed trees is expected to increase if the lake does not dry out regularly (every 1-2 years).

On all transects, *M. cuticularis* and *E. occidentalis* were the only perennial species that displayed flooding tolerance. Both species occur naturally in areas subject to inundation, but the duration of flooding under normal conditions would be much shorter (a few months of the year) than experienced under the elevated water regime of Coomalbidgup Swamp.

Depending on future changes in water regime, all or part of the peripheral sandplain vegetation is expected to regenerate gradually. However, from the differences observed between the two sample dates, species composition and diversity of the regenerated vegetation are expected to differ from the pre-flooding condition. Species such as *B. speciosa* require a fire to trigger seed release, and unless this occurs, recruitment is unlikely. Open disturbed areas,
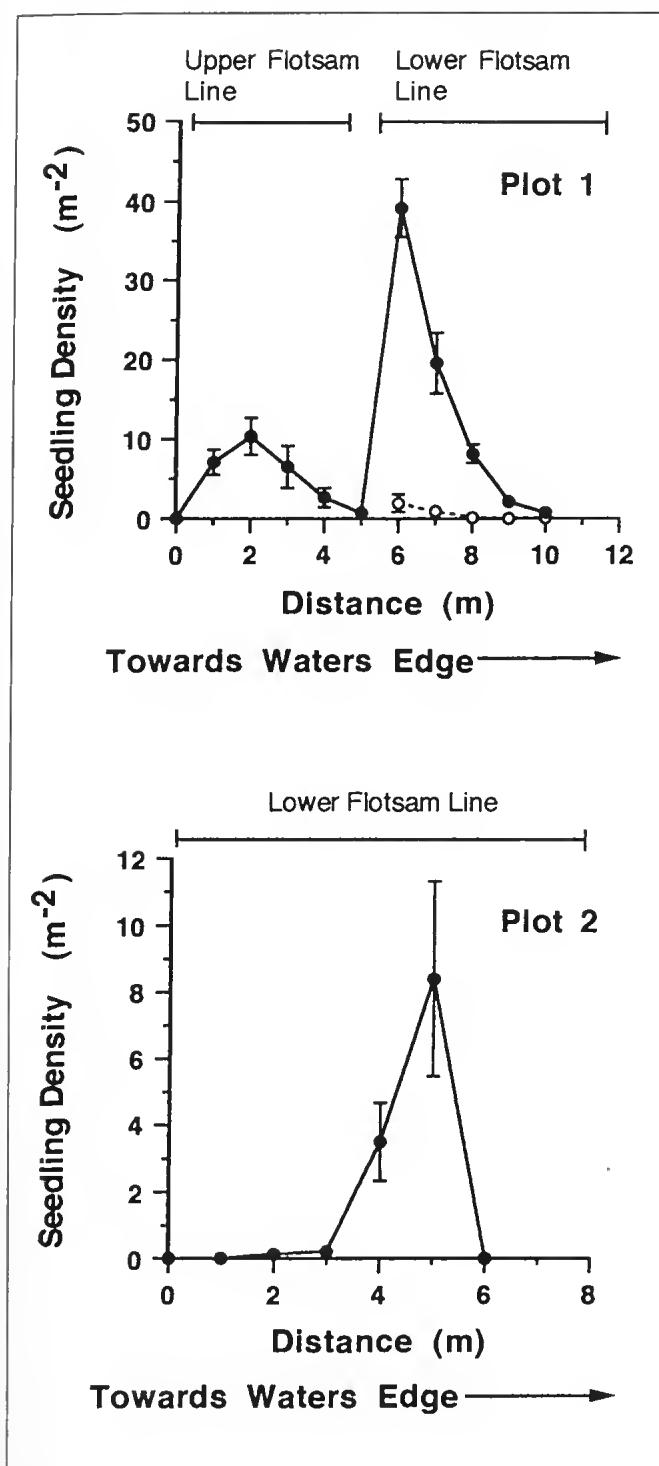
Figure 4. Seedling density along seedling plots 1 and 2. Values are mean ± standard error. ● = *Eucalyptus occidentalis*, O = *Melaleuca cuticularis*

caused by death of vegetation due to flooding, were rapidly colonised by weed species, and dense weed growth may severely restrict recruitment and establishment of native species (Hobbs 1988; Hobbs & Atkins 1988). In some areas where seedlings of *E. occidentalis* germinated amongst dead sandplain vegetation, future survival of the seedlings may depend on an elevated water regime. As noted by the June 1992 observations, seedlings of *E. occidentalis* and *M. cuticularis* continued to establish as the water level receded. With continued inundation and subsequent mortality of the trees on the swamp bed, the distribution of these species may become limited to the littoral zone.

At present, Coomalbidgup Swamp contains relatively fresh to brackish water (≤ 4 ppt). Given that water levels are relatively high, this suggests that with lower water levels, salinity will be greater than 4 ppt. Upon drying, salt in the surface soil of the swamp bed may reach a concentration which will adversely affect the surviving vegetation. Furthermore, with continued groundwater rises and increased runoff from the surrounding catchment, the potential for secondary salinisation is significant. Subsoil salt store levels in the Coobidge Creek area are thought to be high (Bob Nulsen, *pers. comm.*), adding to the future threat of salinisation. Although *E. occidentalis* is relatively tolerant of salinity and waterlogging (Van der Moezel *et al.* 1991), higher salinities are expected to have a detrimental effect on the vegetation of the lake bed and periphery. The adverse effects of higher water levels (without periods of drying) and potential increases in salinity on wetland vegetation in south-western Australia has been documented (Froend *et al.* 1987; Bell & Froend 1990; Froend & McComb 1991). If the disturbance in the water and salt balance of the catchment goes unchecked, the result is a gradual degradation of the low-lying wetland areas. It is clear that at Coomalbidgup Swamp, the death of a significant proportion of the surrounding mature sandplain vegetation occurred during 1986-1992 because of abnormally high water levels and prolonged flooding. Judging from the age of the trees that died during the recent flooding, similar water levels (and duration of flooding) have not occurred within 15-20 years before 1986. Under pristine catchment conditions, flooding events of this magnitude would be rare (Anon 1990).

As studies elsewhere have indicated (Froend & McComb 1991), regular flushing (outflow) of Coomalbidgup Swamp during winter and spring would decrease its total salt load. To reduce mean water depth, ensure regular drying, and increase through-flow, the drainage of the lake may be improved by lowering the elevation of the outflow channel. However, the detrimental effects of increased discharge on other wetlands downstream would need to be determined. Other remedial measures, aimed at the cause rather than the

symptom, may include better water management practices on agricultural land such as improved retention of water on farms coupled with greater water use through transpiration. Management plans for wetlands of conservation value in the Coomalbidgup area should consider the effects of increased surface runoff, elevated groundwater, and associated transport of nutrients and salt, and means of reducing them.

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Rottnest Island artifacts and palaeosols in the context of Greater Swan Region prehistory

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Abstract

The prehistoric record of Rottnest island 19 km offshore the Swan Region, Western Australia, consists solely of three stone artifacts. Two are Eocene fossiliferous chert flakes probably deriving from palaeosols in the Tamala Limestone cliffs at Fish Hook Bay and Little Armstrong Bay. A third is a calcrete flake from a siliceous dune blow-out near Fish Hook Bay. A feldspar pebble *in situ* in a palaeosol intercalated between aeolian calcarenite units at City of York Bay is probably a manuport. The age of the Little Armstrong Bay and City of York Bay palaeosols is estimated to be 15,000 to 50,000 years old. Similarities in pedology and in stratigraphic position suggest that these two palaeosols belong to a single palaeosol unit extending along Rottnest Island's northern shore, a possibility that could give scope to further prehistoric investigations on the island. Prehistoric remains could also be *in situ* in palaeosols and sandy sediments infilling solution pipes and other Tamala Limestone features on the island's littoral and submerged offshore. Of possible archaeological significance are two charcoal concentrations and a pit-like feature *in situ* in the lowermost palaeosol unit in the aeolian calcarenite cliffs at Fish Hook Bay. Charcoal from one concentration is radiocarbon dated *ca.* 18,600 yr b.p. A *Turbo* shell sample from a storm beach deposit emplaced in a wave-cut notch 3.4 m above sea level in the Fish Hook Bay palaeosol is radiocarbon dated *ca.* 5700 yr b.p. The former date is probably erroneous, and the palaeosol is estimated to be 40,000 to 80,000 years old. Factors that could account for the dearth of prehistoric evidence on Rottnest Island are: (1) the island's position near the seaward edge of the emergent continental shelf, which was probably less suitable for human occupation than the shelf's more inland parts; (2) site destruction on the island littoral during the Early to Middle Holocene period of rising and high sea level, when the island was 40% larger in area than now; (3) poor surface visibility on the present-day island. The island's minimal prehistoric record is evidence that it was not occupied extensively prior to its formation; its distance offshore implies that it was not visited by Late Holocene Aboriginal sea voyagers. Palaeoenvironmental and archaeological site distributional data from the emergent continental shelf are used in the appraisal of pre-transgression terrestrial environments and prehistoric occupation in the Rottnest locality and elsewhere in the Greater Swan Region. The Rottnest sites appear to be some of the oldest in the region, and suggest the archaeological potential of Tamala Limestone palaeosols.

Introduction

Rottnest Island, 19 km offshore the Swan Region in south-western Western Australia, was separated from the mainland by glacio-eustatic sea level rise about 6500 years ago (Fig 1; Playford 1983, 1988). The 1900 ha limestone island's prehistoric record consists solely of three stone flakes, two collected in 1984 and the third in 1992, and two pebbles (Table 1). These artifacts are the result of many, mostly unsystematic, searches by numerous archaeologists and other Quaternary investigators since the 1960's. Two of these flakes, and another more problematical specimen, a feldspar pebble also collected in 1992, suggest the archaeological potential of the palaeosol horizons intercalated with the aeolian calcarenite units comprising the greater part of the Tamala Limestone (formerly Coastal Limestone), which is the constituent rock of Rottnest Island, and one of the main Quaternary units in the Perth Basin (Playford 1983; 1988; Playford *et al.* 1976).

The two 1992 finds and the palaeosols at their find spots are described below, along with another recently recorded palaeosol that may be of archaeological significance. We also examine some of the factors that could account for Rottnest Island's extraordinarily sparse prehistoric remains, assess the archaeological potential of the island's littoral and offshore environs, and review palaeoenvironmental data that give insight into the suitability of the Rottnest area for human occupation prior to post-glacial marine transgression.

Fundamental to this assessment of Rottnest island prehistory is the premise that the submerged continental shelf west of the lower reaches of the Swan estuary and environs (Fig 1) is an integral part of the "Greater Swan Region" - an informal term referring to the exposed shelf

Table 1
Summary of 1984 and 1992 Rottnest Island prehistoric stone artifacts and other finds

Specimen	Find spot	WA Museum Accession No.	Aboriginal Sites Dept Reg. No.
1984			
Eocene chert flake	Fish Hook Bay	B5612	S02099
Calcrete flake	Fish Hook Bay, East	B3123	S02099
1992			
Feldspar pebble	City of York Bay	B7712	S02276
Eocene chert flake	Little Armstrong Bay	B7713	S02275
Quartzite pebble	Little Armstrong Bay	B7746	S02275
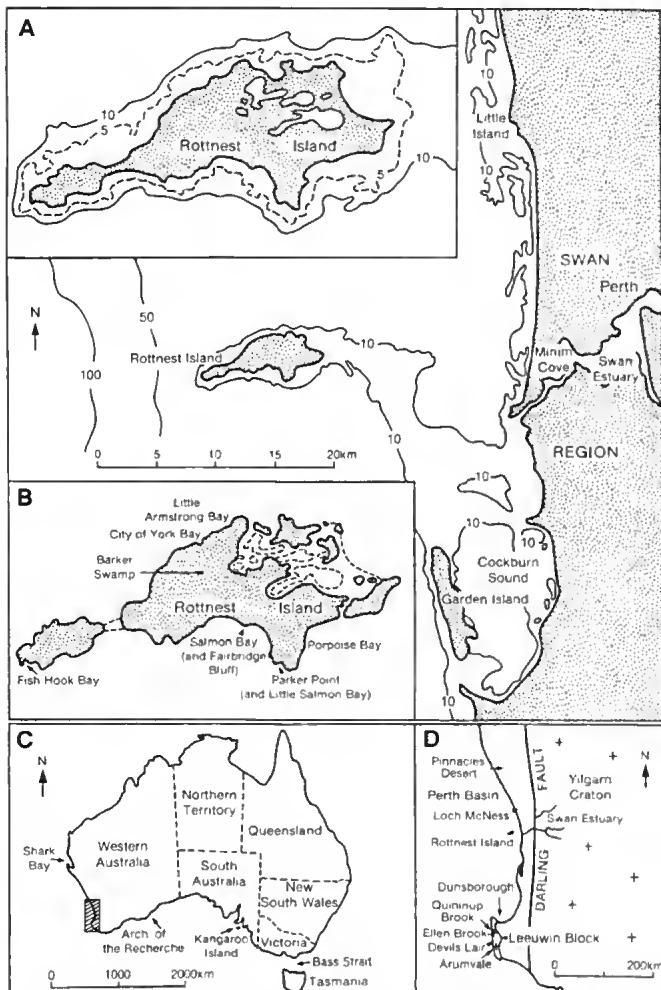
Figure 1. Rottnest island and the Greater Swan Region, Western Australia, showing the 10, 50 and 100 m bathymetric depth contours. Inset A: Rottnest Island showing salt lakes. Island size *ca.* 6500 yr b.p. is based on 5 m depth contour (stippled line). The zone between the 5 and 10 m contours (solid line) indicates approximate land area just before island formation (after Department of Marine and Harbours, WA 1988). Inset B: Rottnest Island at maximum inundation during the Middle Holocene. Modern shoreline and salt lakes indicated by stippled lines (after Playford 1988). Insets C and D: Locality maps.

area accessible to hunter-gatherer populations during the glacio-eustatic low sea levels that persisted through the late Pleistocene and Early Holocene (Chappell & Shackleton 1986, Thom & Chappell 1975). This region extends westward from the Darling Fault scarp through the Swan riverine / estuarine drainage basin to the steepening edge of the continental shelf 10 km west of Rottnest Island, demarcated by the 50 and 100 m depth contours (Fig 1).

Archaeological assessment of pre-transgression human occupation on this and other parts of the submerged shelf off the Indian Ocean coast of southwestern Australia is enhanced by the record of numerous Eocene fossiliferous chert artifact assemblages distributed throughout the emergent Perth Basin and Leeuwin Block (Fig 1D; Glover 1984). Interpreted as deriving from a "concealed western provenance", *i.e.* quarry-factories centred on chert outcrops totally or mostly submerged by glacio-eustatic sea level rise (Glover & Lee 1984), these onshore chert assemblages comprise "the most extensive material record in Australia directly relating to human activities [minimally chert quarrying and knapping] on the now-submerged continental shelves" (Dortch 1991).

Survey aims and methods

Rottnest Island consists mostly of aeolian calcarenite, that is generally covered by heath-vegetated dunes (Hesp *et al.* 1983, Playford 1983, 1988); the salt lakes cover approximately 10 % of the island's area (Fig 1A). Survey for prehistoric sites on the island, mainly carried out by one of us (CED) for the WA Museum, has been largely confined to eroded areas on or near Tamala Limestone coastal cliffs and headlands. These features are important in the survey because intercalated with the aeolian calcarenite units forming these cliffs are calcareous palaeosols which could yield prehistoric occupation material, as was suggested by the provenance and surface condition of an Eocene fossiliferous chert flake found on the island in 1984 (see below). The primary survey aim in 1992 was to test the hypothesis that Rottnest Island palaeosols, occurring within the Tamala Limestone and dating to the Late Pleistocene, contained stone artifacts or other prehistoric remains.

The survey has closely covered an estimated 50% of the palaeosols exposed on the summits and in the faces of the

island's coastal cliffs and headlands, and perhaps 30% of the eroded areas of aeolian calcarenite and palaeosol remnants in the island's interior, particularly those near the salt lakes (Fig 1A). Survey of the smaller areas of siliceous dune blow-outs, that are residual from the weathering of the aeolian calcarenite (Playford 1988: 22), has not been extensive, with at most 20 % of these features having been searched. Very little survey has been carried out in dense heath, in the extant patches of native low forest, or in the much larger areas of tree plantation. Underwater survey of Tamala Limestone features submerged offshore has been done around Parker Point, in Fish Hook Bay and in Little Armstrong Bay (Fig 1B).

The archaeological survey has been concerned solely with locating and recording individual small finds or features relating to prehistoric occupation prior to Rottnest's formation because, as discussed below, it is improbable that the island was later reached by mid-late Holocene prehistoric voyagers from the mainland. Survey has not been orientated toward terrestrial habitats on the island that would seem likely to have invited prehistoric occupation. This is because the present-day island is a scant and heavily eroded remnant of a vast area of emergent continental shelf that was exploited by prehistoric populations in ways that are conjectural, and because the locality's pre-transgression terrestrial habitats probably differed significantly from those existing at the time of European discovery (Backhouse 1993, Storr *et al.* 1959).

Rottnest prehistoric finds and their provenances

The 1984 finds

One of the two stone artifacts found on Rottnest in 1984 is an Eocene fossiliferous chert flake (Fig 2:1) collected from "limestone rubble exposed by the deflation of one or more dune soils" (Dortch & Morse 1984) on an eroding Tamala Limestone cliff-top overlooking Fish Hook Bay (Fig 1B). It is significant that this flake's surfaces (ventral/dorsal faces and butt) are semi-lustrous and only slightly weathered, showing that it has not been subjected long to open-air conditions. The second 1984 find, a deeply weathered calcrete flake (Fig 2:2; Dortch 1991), is from a siliceous dune blow-out on the limestone cliff summit about 300 m east of this bay.

The 1992 finds

The smaller end of the feldspar pebble from City of York Bay (Fig 2:3) has a fracture surface along a cleavage plane that was broken after the stone was rounded; no archaeological significance is attributed to this fracture. The nearest known sources of feldspar pebbles deriving from the Yilgarn Craton are mainland alluvial gravels in the vicinity of the Darling Fault, 50 km east of Rottnest Island (Fig 1D). This feldspar pebble (weight 12.41 g, maximum length 33 mm) is in the size range of emu crop stones (pers. comm.: R Johnstone, Department of Terrestrial Vertebrates, WA Museum). However, the considerable distance between Rottnest Island and the nearest known feldspar sources, and this pebble's relatively large size suggest to us that it is more likely to be a manuport (*i.e.* an object transported through human agency) than a crop stone.
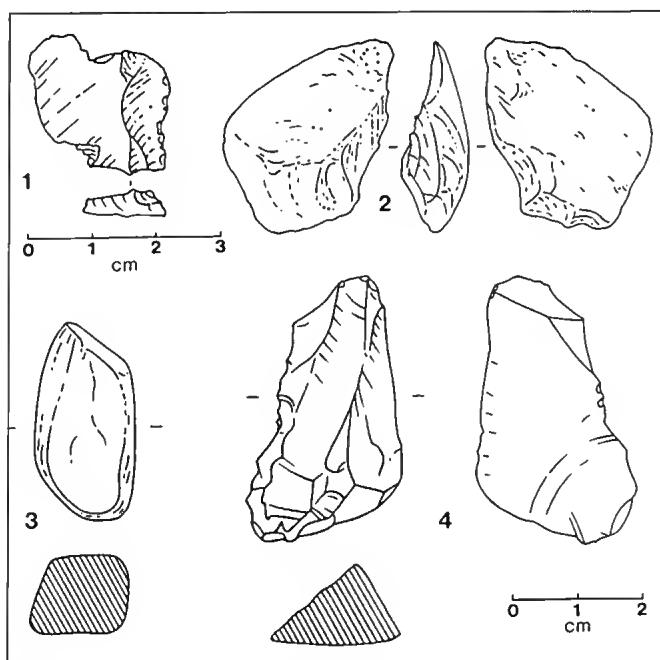
Figure 2. Prehistoric finds from Rottnest Island. 1984 specimens: 1 Eocene fossiliferous chert flake from Fish Hook Bay; 2 calcrete flake from 300 m East of Fish Hook Bay. 1992 specimens: 3 feldspar pebble from City of York Bay; 4 Eocene fossiliferous chert flake from Little Armstrong Bay.

The Eocene fossiliferous chert flake from Little Armstrong Bay (Fig 2:4) weighs 6.98 g, and has a maximum length of 44 mm. It has a diffuse bulb of percussion and a linear butt, features characteristic of bipolar percussion. The two prominent flake scars covering the dorsal face have been produced by blows against its distal end, probably by means of counter-percussion, as suggested by the very small flake scar facets and crushing that have removed the proximal ends of the prominent flake scars. The flake has a prominent notch midway along its left edge' produced deliberately by three or more blows. The flake's surface is uniformly matt, finely porous, and light-hued, whitish-buff, similar to the colour of the sandy palaeosol from which it probably derives (see below). Like the 1984 chert flake (Fig 2:1), the 1992 flake " ... appears to have been buried in a stable deposit for most of the time since it was discarded" (Dortch & Morse 1984).

A weathered quartzite pebble (Table 1: B7746) was collected *in situ* in the palaeosol at Little Armstrong Bay 1 m east of the chert flake's find spot. This piece is conceivably a manuport, although its very small size (weight 1.26 g; maximum dimension 16 mm) suggests that it was naturally transported; for example, it could be a bird crop stone.

The City of York Bay and Little Armstrong Bay find sites

The two 1992 prehistoric finds are from aeolian calcarenite cliffs at City of York Bay, and at Little Armstrong Bay, 1100 m further north-eastward along the northern shore of the island (Fig 1, Table 1). Each cliff face features a prominent palaeosol intercalated between aeolian calcarenite units. The feldspar pebble was found *in situ* in the City of York Bay palaeosol (Fig 3a). The chert flake from Little Armstrong Bay, however, was not *in situ*, but found lying on a 10 cm-thick deposit of fine carbonate sand covering a calcarenite ledge at the foot of the prominent palaeosol exposed in a 1 to 1.3 m-

high section in this cliff face (Fig 3b). This sand closely resembles that in the palaeosol, and almost certainly is eroded from the palaeosol section, as is the case with the chert flake. Less likely derivations for the flake are the summit of the cliff, or the aeolian calcarenite unit forming a 1 m-wide overhang above the palaeosol section. Sieving of
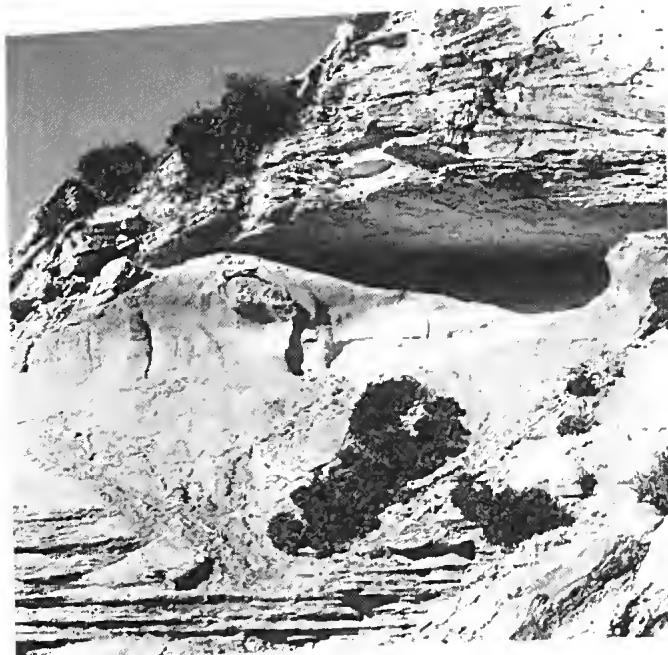
Figure 3. Tamala Limestone cliffs on Rottnest Island, showing cross-bedded aeoline calcarenite palaeosols: **TOP** City of York Bay, the position of the feldspar pebble (Fig 2: 3) found *in situ* is in the shaded area beneath the calcarenite overhang; **BOTTOM** Little Armstrong Bay, 15 cm scale in centre of palaeosol section.

approximately 100 litres of the loose sand on which the flake was lying yielded no archaeological finds, but did reveal small calcareous nodules, rhizotubules and land snail shells (*Austrosuccinea* sp.), as found in the palaeosol.

The palaeosols at both these find spots display moderately deep (*ca.* 0.6 m), light-grey A horizons with diffuse contacts to a lower C horizon; no B horizon is present. The A and C horizons in the Little Armstrong Bay palaeosol are formed in fine carbonate sand, with very small fraction of fine-medium quartz grains dispersed throughout. The City of York Bay palaeosol has an A horizon that is 60% fine carbonate sand and 40% fine-medium quartz sand; its C horizon consists of equal amounts of fine-medium carbonate sand and medium-coarse, well-rounded quartz grains. In both palaeosols, small carbonate nodules and rhizotubules (maximum dimension - 1 cm) are present in frequencies estimated at 100 per 1 m^3. Land snails (*Austrosuccinea* sp.) are common in the upper two thirds of the A horizon of each palaeosol.

The pale cream-white C horizon in each palaeosol appears to be parent material lacking laminae or bedding planes. Observations of presumed Early to Middle Holocene calcareous soils on Rottnest indicate that the C horizon develops via chemical breakdown of the laminated limestone as the A horizon forms. The slightly cemented C horizons have the same colour, texture, and grain size distributions as the underlying, laminated aeolian calcarenite. Limited organic development or leaching takes place in the A horizon presumably due to low rainfall (*ca.* 715 mm p.a.), high exposure, semi-arid vegetation with limited turnover, a Mediterranean climate and limited soil fauna.

The palaeosols at the City of York Bay and Little Armstrong Bay find spots are thus pedogenetically very similar, and their stratigraphic positions within each cliff face, and heights above sea level are also much the same (Table 2; Fig 3a, b). Closely resembling these two soil horizons are ones intercalated with calcarenite units at Charlotte Point and at the east end of Catherine Beach, 300-400 m east of the City of York Bay find spot. The Little Armstrong Bay palaeosol extends eastward along the shore about 300 m, and several palaeosol horizons exposed in coastal cliffs several hundred metres further to the east may be part of this same unit. While we stress that the palaeosols cannot be traced laterally very far, the City of York Bay and Little Armstrong Bay palaeosols appear to belong to a single soil unit extending more than 1500 m along the northern shore of the island. Other exposed palaeosols in the cliffed series of headlands near the western end of the island, 3 to 5 km from City of York Bay, may also belong to this putative soil unit. This is a question of some consequence, since the widespread distribution on the island of a palaeosol having potential for at least rare finds would greatly enhance the chances for discoveries of prehistoric remains.

Estimated age of The City of York Bay and Little Armstrong Bay palaeosols

The City of York Bay and Little Armstrong Bay palaeosols are overlain by thick aeolian calcarenite units. These are truncated and cliffed lee slope and slipface beds, the foreset beds having been removed by wave action. Even if these aeolian units were formed as steep, climbing dunes, it is highly unlikely that they were formed at modern or mid-Holocene sea levels. This is because the dune crests are also absent, and if one projects the crests and windward (foreset) slopes seaward, the toe of the windward slopes would extend below sea level. The dune units were thus formed

during Pleistocene lower sea levels when the glacial beach was some distance north and west of Rottnest. The age range for the underlying palaeosols is therefore speculated to be *ca.* 15,000 to 50,000 years old (Chappell & Shackleton 1986; Thom & Chappell 1975). This estimate is further supported by the fact that the overlying aeolian dune units are lithified, whereas younger dunes mantling the Tamala Limestone are poorly lithified or unconsolidated. Many of these younger dunes have steep seaward faces, and appear to have formed during or after the latter stages of post-glacial marine transgression.

carbonate sand, and has a very deep (2.3 m) A horizon varying in colour from dark to light brown (mean 7.5 YR 5/ 3: brown). The soil contains *Leptopius* pupal cases, rare carbonate nodules, and in its uppermost 1 metre *Austrosuccinea* shells. The A horizon has a diffuse boundary with a 1.2 m thick lower 'unit' (tentatively designated as a C horizon) showing intense rhizotubule development.

In the middle of the A horizon are two charcoal concentrations separated by a pit-like structure (Fig 4a). The charcoal concentrations are approximately 70 cm from the

Table 2

Physical description of palaeosol horizons at City of York Bay, Little Armstrong Bay and Fish Hook Bay. Elevation is a.s.l. (top of a horizon).

	City of York Bay	Little	Fish Hook Bay
Munsell colour			
A horizon	10 YR 7/2	10 YR 7/2	7.5 YR 5/3
C horizon	10 YR 8/1	5 Y 8/1	5 Y 8/1
grain lithology			
A horizon	carbonate/quartz	carbonate	carbonate
C horizon	carbonate/quartz	carbonate	-
grain size			
A horizon	fine-medium sand	fine sand	fine sand
C horizon	fine-medium-coarse	fine	-
organic content	nil	nil	scattered or concentrated charcoal fragments
A horizon thickness	0.8-1.2 m	0.6 m	2.3 m
elevation	7 m	9 m	4 m

The Fish Hook Bay Site

Most of the palaeosol sections exposed in cliff faces along the northern shore of Rottnest Island have been searched for archaeological material, as have many palaeosol sections on the island's southern shore. Apart from the finds listed in Table 1, the only other possible prehistoric remains recorded so far are in a palaeosol section at the base of the 20 to 25 m - high calcarenite cliffs in the eastern corner of Fish Hook Bay (Table 2). No other exposure of this palaeosol, which is at the base of a series of three aeolian calcarenite units intercalated with two other palaeosols, has been identified at this bay or elsewhere on the island.

This lowermost Fish Hook Bay palaeosol is exposed beneath a calcarenite overhang in an eroded section 3.5 m thick; the unit is concealed from view by an 8 m - high mass of huge limestone blocks and scree material fallen from the face of the overlying cliff. A wave-cut notch is formed in the palaeosol at *ca.* 3.4 m above sea level, and its base is being eroded by wave or tidal action to form an active sea cave of unknown length. The south-facing palaeosol is exposed in a 10 m long section. It consists of very slightly cemented fine

top of the A horizon, and about 70 cm apart. Each consists of very friable charcoal fragments 2-15 mm in maximum dimension. The northernmost, best-defined concentration is a horizontal band 65-70 cm long, and about 1 cm thick; the charcoal fragments forming this band are not contiguous but are separated by sand fill, showing that the charcoal and the sand were deposited at the same time (Fig 4b). This charcoal band shows no signs of having been burnt *in situ*, as it has no associated white ash, or fire-crazed and scorched sand grains characteristic of hearths and other fire zones in primary position. The other charcoal concentration is more widely redistributed, and consists of several isolated charcoal fragments forming a horizontally oriented cluster about 30 cm long and 15 cm high. Minute charcoal fragments are present in the palaeosol section above the two charcoal concentrations but not below. Whether the charcoal in these concentrations derives from bush fires, or from hearths or other fires associated with human activities is open to question.

The pit-like structure (Fig 4a) is 50 cm wide at its top, and measures 45 cm from top to bottom. The feature is defined by its fill of dark brown sand, and by a thin carbonate encrustation

Figure 5. Fish Hook Bay wave-cut notch and storm beach deposit, elevation *ca.* 3.4 m above sea level. Feature consists of imbricated calcarenite cobbles emplaced in palaeosol. At upper left of cobble deposit is 15 cm scale. The arrow indicates the position of the dated *Turbo* shell.

Figure 4. Fish Hook Bay palaeosol: **TOP** northernmost charcoal concentration and pit-like structure; **BOTTOM** close-up of charcoal concentration in 4a. In both photographs is a 15 cm scale.

on its right side and a line of very small calcarenite nodules on the other. It could be a burnt tree root or possibly an Aboriginal fire pit. The two charcoal concentrations and the top of this structure are much the same height, suggesting that all three are contemporaneous.

The palaeosol has been notched by wave action subsequent to its formation and to the deposition of the overlying 20-25 m-high aeolian calcarenite cliff. A storm beach deposit, 2.3 m long and 30 cm thick, and comprising small (5-8 cm) to large (30 cm) calcarenite cobbles is emplaced in the palaeosol where the wave-cut notch broadens into a bench at the southern end of the section, approximately 3.4 m above sea level (Fig 5). A few marine mollusc (*Turbo*) shells are *in situ* among the imbricated calcarenite cobbles. The beach deposit is partly buried by collapse of the overlying calcarenite units, which formed a wide overhang above the storm beach and palaeosol, judging by the massive amounts and size of the calcarenite blocks accumulated in front.

Age estimation of the Fish Hook Bay palaeosol

Judging by its stratigraphic situation, the Fish Hook Bay palaeosol is potentially one of the oldest of these features on Rottnest. However, a radiocarbon sample of charcoal from the northernmost charcoal concentration (Fig 4a) gave an age of 18,660±250 yr b.p. (SUA 3030), which we consider to be erroneously young presumably as a result of contamination by younger carbonate. Although the sample was pre-treated to remove younger carbonate by boiling in dilute hydrochloric acid, because of its small size it was only lightly pre-treated by soaking in alkali-prophosphate to remove humic acids possibly present.

Radiocarbon age of the Fish Hook Bay storm beach deposit

Our interpretation of the wave-cut notch and storm beach deposit shown in Fig 5 as one of the many Rottnest shoreline features created by Middle Holocene high sea levels relative to the island's littoral and salt lake shorelines (Playford 1983, 1988, see below) is supported by a radiocarbon date of 5,730 ±60 yr B.P. (SUA 3037) for a whole *Turbo* shell from the storm beach deposit. A 1-2 m storm surge occurring when sea level was *ca.* 2 m above present level can easily account for the storm beach deposit's 3.4 m elevation.

Archaeological potential of shoreline and offshore zones

The oldest known Tamala Limestone on Rottnest island is exposed just at and below mean sea level at Fairbridge Bluff in Salmon Bay (Fig 1). Here, Tamala Limestone underlies the partly-emergent Rottnest limestone coral-reef unit (Playford 1988), dated by uranium-thorium technique to 132,000 ±5000 yr b.p. (Szabo 1979). This date suggests that the oldest Tamala Limestone shoreline features on the island, or submerged at shallow depths offshore, could pre-date the earliest human presence in this region. However, exposed at many places on Rottnest Island's mainly rocky shores are cemented soil horizons and sandy sediments that have infiltrated the cavities of solution pipes and other older

limestone structures. At Little Armstrong Bay, for example, part of a palaeosol is exposed in an intertidal erosion pool. This palaeosol, which has in it rhizotubules and *Leptopius* weevil pupal cases, is intercalated between wave-eroded units of aeolian calcarenite. The lowermost palaeosol unit exposed at City of York Bay is approximately 1 m above sea level. These shoreline palaeosol units and sandy infillings are potentially places where isolated stone artifacts or other relevant finds could be located, both above and within the 2.4 m high inundation zone dating to the Middle Holocene transgression (see below).

Archaeological investigation of Rottnest Island rocky shorelines, including test excavation of unconsolidated sand filling the hollows of two large solution pipes just above sea level at the south-west end of Porpoise Bay, has not revealed any prehistoric material or terrestrial fossils (Figs 1B, 6). The partly excavated solution pipe illustrated rests on a 30-cm-thick reddish indurated palaeosol with rhizotubules, whose base is *ca.* 30 cm above sea level. The sediment excavated from these two pipes is a fine, iron-stained (reddish-yellow: 7.5YR 6/8) quartz sand similar to that of the Spearwood Dune System, which is one of the major constituents of the mainland Tamala Limestone (McArthur & Bettenay 1974), though not recorded on Rottnest Island. The presence on Rottnest of these sands is archaeologically significant, since some late Pleistocene to Middle Holocene assemblages of Eocene chert artifacts in the emergent Perth Basin are associated with Spearwood dunes, *e.g.* in the Pinnacles Desert 170 km north of Perth (Fig 1D; McNamara 1983), at Minim Cove near the mouth of the Swan Estuary (Fig 1; Clarke & Dortch 1977) and at Dunsborough (Ferguson 1982), as well as with dune soils on the western parts of the Leeuwin Block (Fig 1D) closely resembling and occupying the same sequential position as those of the Spearwood Dune System, *e.g.* at Quininup Brook (Ferguson 1981), Ellen Brook (Bindon & Dortch 1982), Devil's lair (Dortch 1984) and Arumvale (Dortch & McArthur 1985).

Figure 6. Partly excavated Tamala Limestone solution pipe, south-western end of Porpoise Bay, Rottnest Island, WA.

Playford (1988) notes that sub-aerial features, including aeolian calcarenite, palaeosols and limestone solution pipes, extend below sea level at many localities around Rottnest Island, probably reaching depths of 70 m or more. For example, there are a dozen solution pipes, 1.5 to 2.0 m high

and 0.4 to 0.7 m wide, rising from the sea floor at depths of 3-5 m offshore Parker Point and Little Salmon Bay (Fig 1B). These Rottnest solution pipes closely resemble the one in Fig 7, photographed among a large number of submerged solution pipes surrounding a massive calcrete horizon in water 3 m deep near Little Island, two km offshore the mainland, and 25 km north-east of Rottnest Island (Fig 1). Although it is improbable that these features have much potential for archaeological survey, they are still part of a pre-transgression landscape traversed by human groups.

Figure 7. Submerged solution pipe in an outcrop of Tamala Limestone, near Little Island, offshore the Swan Region, W.A. (Photographed by Clay Bryce, WA Museum, Perth).

Discussion

Three factors are probably significant in accounting for Rottnest Island's extremely sparse prehistoric record.

1. The paucity of prehistoric finds may largely reflect late Pleistocene/Early Holocene occupation patterns in the Greater Swan Region. One of us (Dortch 1991) has proposed that the pre-transgression site distribution on the emergent, western half of the continental shelf was similar to that recorded in the present coastal plain (approximating the Perth metropolitan region). Here, Aboriginal occupation during the latter half of the Holocene, and probably during earlier millenia, was concentrated in the coastal plain's eastern, inland half, where abundant surface water and diverse resources are available (Hallam 1987). As suggested then, the outer, western part of the emergent shelf was not much used by prehistoric groups, and occupation instead was concentrated around wetlands and lakes in the shelf's inner parts, a likely example being the terminal Pleistocene - Early Holocene lagoon delineated by the 10 m contour in the central part of Cockburn Sound (Fig 1; Churchill 1959, Dept of Marine and Harbours 1988, Searle and Seminiuk 1985).

2. Middle Holocene high sea level (Thom and Chappell 1975), including sea level rise that reduced the newly formed island's area by more than a third following its

time of initial formation, and continued to rise, thereby inundating the newly formed island's low-lying areas, probably helps account for Rottnest Island's extremely sparse prehistoric record. This is because any intensive human occupation of the Rottnest locality shortly before its becoming an island is likely to have been concentrated at low elevation along marine shores, or in the vicinities of the island's swamps, which then would seem to have been fresh-water, judging by new evidence from Barker Swamp (Fig 1B) discussed below, or around the salt lakes, which perhaps also were brackish or fresh-water at that time.

Bathymetric contours of the sea floor between Rottnest Island and the mainland (Dept of Marine and Harbours 1988) imply that the post-glacial isthmus connecting the two was severed when rising seas reached a level 5-10 m below present mean sea level (see 10 m depth contour line in Fig. 1, and the 5 and 10 m contour lines in Fig 1A). Island formation with the sea at that level means that at its initial separation ca. 6500 years ago, Rottnest was forty per cent larger in area than it is now (Churchill 1959, Department of Marine and Harbours 1988). However, continuing sea level rise apparently within a few centuries inundated the newly formed island's shores, reaching a peak ca. 5900-4800 years ago, when sea level relative to the island is estimated to have been about 2.4 m higher than at present (Playford 1983, 1988). At that time, most of the present-day Rottnest shoreline was inundated, and the area of the island's salt lakes was a marine embayment sheltered from the open sea by stacks and islets (Fig 1B). The evidence for these high sea levels relative to Rottnest Island consists of a number of radiocarbon-dated molluscan shell deposits located in modern quarry sites in the island's interior, or associated with wave-cut platforms and notches on the island's salt lake shorelines (Playford 1988). This record is now supplemented by the above noted 5700 yr b.p. elevated storm beach deposit emplaced in the Fish Hook Bay palaeosol (Fig 5). Although no archaeological features are associated with any of these elevated shoreline features and deposits, their presence may help to explain the dearth of Rottnest Island prehistoric sites. Playford (1988) has suggested that the Middle Holocene high sea levels relative to Rottnest Island may be more the result of localised tectonism than of glacio-eustatic sea level rise, continuing after sea level had reached its present height. Whatever its causes, inundation on this scale, preceded by the loss of more than a third of the newly formed island's area, has a destructive potential that cannot be ignored when assessing Rottnest Island prehistory.

3. Poor surface visibility must in part account for Rottnest Island's sparse prehistoric record, with most of the island's Tamala Limestone (including calcareous soil horizons and quartz residual dunes) covered by thick scrub or late Holocene dunes that restrict archaeological survey on the island to cliffs and other eroded Tamala Limestone features - particularly palaeosols, and to dune blow-outs and road cuttings. However, it is uncertain whether widespread exposure of subsurface features and ground surfaces on the island would reveal extensive or numerous prehistoric sites.

Prehistoric voyages to Rottnest Island?

Prehistoric Aboriginal voyages to Rottnest Island can be virtually discounted. For several Australian coastal regions there are ethnohistoric data relating to the seaworthiness of various kinds of Aboriginal watercraft. These data (Jones 1977) show that Rottnest is much too far offshore to have been within feasible voyaging range from the mainland. This is assuming that there was ever incentive to undertake a 19 km voyage to an offshore island in south-western Australia, a region for which there are plentiful ethnohistoric data for estuarine shoreline fishing (e.g. Moore 1978 [1884]), though where there is no indication of Aboriginal watercraft of any kind (Dortch & Morse 1984), and nothing to suggest prehistoric voyages to any offshore island, including Garden Island separated from the mainland by a 2 km-wide strait (Fig 1; Dortch & Morse 1984).

However, in considering possible prehistoric human visits to Rottnest following its formation, it is necessary to discuss the putative shell midden reported on the island by Hughes et al. (1978), which is a bed of marine mollusc shells (predominately Turbo, with a few limpets) on a low ledge near Parker Point (Fig 1B). This particular shell bed is considered to have accumulated through Pacific Gulls dropping shells in order to break them (Playford 1988), as observed on Rottnest Island by Teichert & Serventy (1947) and by Storr (1965). One of us has suggested that the shell bed is a storm beach deposit (Dortch 1991). We concur that the Parker Point shell bed probably is naturally accumulated, by one or perhaps by both of the processes noted above. Moreover, the low elevation of the deposit (1 to 3 m above sea level) places it within the range of the earlier noted Middle Holocene high sea levels that significantly eroded the island littoral. Therefore, this intact shell bed post-dates these high sea levels, and if it is a midden would presumably result from a human presence on the island following its formation. However, the weathered appearance of the shells in the upper part of the Parker Point deposit suggests to Hughes et al. (1978) that it is prehistoric rather than having "accumulated as a result of of shell gathering by Aboriginal convicts confined to the island late last century."

If the Parker Point deposit is a shell midden, it would be surprising that a deposit of this size, at least 100 times greater in mass than any of the 10 extremely small shell midden deposits recorded along south-western Australia's coastline - extending 1800 km from latitude 29° South to longitude 123° East (Dortch et al. 1984), would be found on a small, arid and relatively distant offshore island that otherwise has yielded absolutely minimal prehistoric remains of any kind (Table 1; cf. above comments on watercraft). The regional evidence for Aboriginal mollusc exploitation "is decidedly sparse and sometimes equivocal;" (Dortch et al. 1984), though this comment does not apply to the Parker Point shell deposit, which is prolific and almost certainly natural. (An archaeological examination of another Rottnest Island shell deposit resembling a midden has been made by Bindon et al. (1978).

Palaeoenvironmental considerations

During the last glacial maximum, with the sea at its lowest levels (Chappell & Shackleton 1986, Thom and Chappell 1975), Rottnest can reasonably be asumed to have been a

waterless series of resource-poor limestone ridges and dunes. At that time, the only parts of Rottnest that may have been attractive for human groups are the present-day salt lakes (Fig IB), which are probably karst structures (Playford 1988). Prior to sea level rise, these presumed caves or dolines could have featured rainwater pools.

Although the terrain on Rottnest and other parts of the outer shelf may have been uninviting during the glacial maximum, by the Early to early Middle Holocene, the shelf's still emergent parts would seem to have been suitable for human occupation, in part as a result of coastal plain water table rise consequent to glacio-eustatic sea level rise. These favourable conditions are suggested by radiocarbon dated biotic data from the mainland and from Rottnest Island. A pollen sequence for Loch McNess near the coast 50 km north of Perth (Fig1D) shows little change in local vegetation (mainly *Eucalyptus* woodland interspersed with swamp dominated by sedge communities) from 9000 yr b.p. until the present (Newsome & Pickett 1993). A corresponding record is provided by a radiocarbon dated sequence of peat, pollen, aquatic molluscs and ostracods (Backhouse 1993) from the lower part of a core at Barker Swamp, Rottnest Island, which shows that about 7,200 years ago and continuing for several centuries thereafter, this 1 ha swamp was an open freshwater lake surrounded by "sedges and *Callitris* [native pine] low forest, with a restricted jarrah / tuart [*Eucalyptus marginata/E. gomphocephala*] woodland present nearby" . The Barker Swamp record is to some extent supported by previous, much less well documented evidence consisting of the remains of a grass-tree (*Xanthorrhoea* sp.) radiocarbon dated *ca.* 7,000 yr b.p, and collected from a bore at an unknown locality on Rottnest Island (Churchill 1960). *Xanthorrhoea* is an understorey plant in jarrah and tuart woodland (Beard 1981), and remains of these species are also dated 7,000 yr b.p. in the Barker Swamp core (Backhouse 1993). Barker Swamp is is less than 1 m above sea level; its core record suggests that 7000 years ago, some or all of the island's other seven swamps were fresh-water bodies, as may have been the present-day salt lakes. This core record is evidence that the Rottnest area offered congenial conditions for human occupation for at least several centuries prior to its separation from the mainland.

The use of palynological and other palaeoenvironmental data, as well as submerged shelf topography and archaeological site distributions (Dortch 1991), in assessing former terrestrial environments and occupation patterns, as outlined here for the Greater Swan Region, has even greater applicability in those regions where the presence of numerous or extensive Pleistocene/ Early Holocene archaeological sites on offshore islands or on mainland coasts leaves little doubt that the adjacent submerged shelf was an integral part of the landscape exploited by pre-transgression hunter-gatherer populations. In southern Australia (Fig 1C), these regions include Shark Bay (Bowdler 1990), the Archipelago of the Recherche (Dortch & Morse 1984), Kangaroo Island and neighbouring mainland peninsulas (Lampert 1981), and Bass Strait (*e.g.* Jones 1977).

Significance of the Rottnest prehistoric finds

The Rottnest Island prehistoric finds (Table 1) are all problematical, the two chert flakes because they were not found *in situ*, and the feldspar pebble because of its less than

absolute cultural association. The calcrete flake (Fig 2:2) shows the archaeological potential of the Rottnest residual siliceous dunes; it is relevant that 117 limestone (mostly calcrete) artifacts were recovered from the late Pleistocene deposit at Devil's Lair cave (Fig 1D; Dortch 1984). The feldspar pebble (Fig 2: 3) and the two Eocene fossiliferous chert flakes (Fig 2:1, 4) clearly pre-date Rottnest Island's formation during the early Middle Holocene. The two flakes' presence on Rottnest island, like the two Eocene fossiliferous chert flakes from Garden Island and the many hundreds of others from the Archipelago of the Recherche (Fig 1C; Dortch & Morse 1984), is in keeping with their presumed age and derivation from chert outcrops on the emergent shelf.

These rare prehistoric finds to date imply that the pre-transgression land mass broadly synonymous with Rottnest Island was probably never occupied intensively. If such occupation did take place, the archaeological remains have been destroyed by Middle Holocene sea level rise and continuing marine conditions, or are buried beneath marine / lacustrine sediments, dune sands or some of the island's aeolian calcarenite units.

The potential of palaeosols within Tamala Limestone sequences on Rottnest Island for yielding rare archaeological finds is now apparent, and this potential may extend to palaeosol units in the Tamala Limestone throughout the Perth Basin and Leeuwin Block. The presence of what may be a single palaeosol unit extending for several km along Rottnest Island's northern shore offers perhaps the best opportunities for further prehistoric investigations on the island. The cultural finds described here and the estimated age of the palaeosols at the Little Armstrong Bay and City of York Bay find sites are suggestive of an age for prehistoric occupation in south-western Australia equalling or exceeding that shown for Devil's Lair - *ca.* 33,000 yr b.p. (Dortch 1984) and the Upper Swan site - *ca.* 38,000 yr b.p. (Pearce & Barbetti 1981). Further investigations on Rottnest should clarify the ages of some of these palaeosols, and verify the occurrence of prehistoric material within them.

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Recent Advances in Science in Western Australia

Earth Sciences

Strike-slip faulting, previously thought to be of minor importance, is shown by R Iasky, of the Geological Survey of WA, to have had a major impact on the evolution of the southern Perth Basin. Three major periods of tectonism re-activated major faults: right-lateral strike-slip motion along the Darling Fault in the Late Permian-Triassic led to the rise of the Harvey Ridge; tectonism with associated left-lateral strike-slip motion along the Dunsborough Fault in the Jurassic resulted in deposition and faulting; separation of Australia from India in the Early Cretaceous resulted in uplift with a predominantly tensional, but also some oblique-transcurrent, right-lateral, faulting.

Iasky R P 1993 A structural study of the southern Perth basin. Geological Survey of Western Australia. Report 31.

Archaean mafic and ultramafic volcanic rocks between Menzies and Norseman, which include massive and pillowed basalts and a komatiite unit, are grouped geochemically by P Morris, of the Geological Survey of WA, into a lower and an upper basalt group. The rocks were erupted subaqueously in deep water, probably in an elongate rift near an active arc.

Morris P A 1993 Archaean mafic and ultramafic volcanic rocks, Menzies to Norseman, Western Australia. Geological Survey of Western Australia. Report 36.

R Horwitz and E Ramanaidou, of the CSIRO Division of Exploration Geoscience, describe how a hiatus in parts of the Jeerinah Formation in the Hardey Syncline region was probably caused by submarine slumping during sedimentation. Removal by slumping, and redeposition westwards, could account for olistostromes previously recorded in the Jerrinah Formation on the southern rim of the Wyloo Dome.

Horwitz R C & Ramanaidou E R Slumping in the Marra Mamba Supersequence Package in the Southern Hamersley Province, Western Australia. Australian Journal of Earth Sciences 40:339-344.

Researchers from Curtin University and the Geological Survey of WA have measured Rb-Sr dates of 430-500 Ma for biotites in granite and gneiss in a 30-55 km wide belt at the western edge of the Yilgarn Craton, between Perth and Harvey. A transition zone 15-40 km wide separates this belt from an eastern chronological plateau where biotite dates are 2300-2600 Ma (marginally younger than whole-rock dates which average 2550 Ma and persist to the western edge of the craton). The 430-500 Ma dates probably represent resetting during uplift in the Early Palaeozoic.

De Laeter J R & Libby W G 1993 Early Palaeozoic Rb-Sr dates in the Yilgarn Craton near Harvey, Western Australia. Australian Journal of Earth Sciences 40:445-453.

Researchers based in Canberra (AGSO and ANU) describe how the Canning Basin contains several Zn-Pb sulphide prospects and deposits in Devonian reef complexes on the Lennard Shelf and in Ordovician and Silurian marine sequences on the northern margin of the Willara Sub-basin. The basin contains highly saline waters whose dominant component is bittern water probably expelled from marine evaporites in the Silurian Carribuddy Formation. These bitterns are similar in chemical composition to metal-rich bitterns from the Mississippi Salt Dome Basin, and it is assumed that the Canning Basin bitterns were metalliferous and a component of the ore-forming fluids.

Ferguson J, Etminan H & Ghassemi F 1993 Geochemistry of deep formation waters in the Canning Basin, Western Australia, and their relationship to Zn-Pb mineralization. Australian Journal of Earth Sciences 40:471-483.

U-Th-Pb dating of zircons from Late Archaean granites in the Norseman region shows the existence of two distinct magmatic episodes, suggesting two periods of regional metamorphism at about 2660 and 2685 Ma. Large regional tonalitic and granodiorite plutons were emplaced between 2685 and 2690 Ma, while large regional granite and small tonalite and leucogranite plutons that intrude greenstones are 2660-2665 Ma.

Hill R I & Campbell I H 1993 Age of granite emplacement in the Norseman region of Western Australia. Australian Journal of Earth Sciences 40:559-574.

J Clarke, of the Western Mining Corporation, describes how the Lefroy and Cowan palaeodrainage systems were probably initiated in the pre-Jurassic, and both flowed to the north and east. The Cowan system reversed prior to Jurassic deposition in the Bremer Basin, to flow south to the Bremer Basin and the Lefroy palaeodrainage flowed east to the Eucla Basin. The first drainage channel fill occurred during the Eocene under fluvial to marine conditions. In post-Eocene times, the drainage channels fragmented into a series of lakes. From the Pliocene onwards, increasing aridity led to the deposition of gypsum in both Lake Cowan and Lake Lefroy.

Clarke J D A 1994 Evolution of the Lefroy and Cowan palaeodrainage channels, Western Australia. Australian Journal of Earth Sciences 41:55-68.

Life Sciences

Patterns amongst Australian mammals and lizards of termite eating were examined by M Abensperg-Traun, of the Division of Wildlife and Ecology, CSIRO, Midland. In the arid and semi-arid zones, most termite consumers are lizards; dasyurid marsupials consume relatively few termites (<10% of their diet). It is argued that the low and variable rainfall of inland Australia results in seasonality of termite abundance, and so the specialized termite eaters are energy-frugal lizards.

Abensperg-Traun M 1994 The influence of climate on patterns of termite eating in Australian mammals and lizards. Australian Journal of Ecology 19:65-71.

Experimental studies of *Eucalyptus marginata* seed dispersal and mortality, by G Stoneman and B Dell of Murdoch University, and N Turner of the CSIRO Division of Plant Industry, indicated that small vertebrates substantially reduce emergence, whereas invertebrates only slightly reduce emergence. Seed removal was insignificant when covered by soil, or with an understorey and litter present to make the

seed less visible. Seed mortality was lower for sites with the overstory removed or a greatly disturbed seedbed. Most mortality was due to water deficit in late spring and summer, and some was due to pathogenic fungi.

> Stoneman G L & Dell B 1994 Emergence of *Eucalyptus marginata* (jarrah) from seed in Mediterranean-climate forest in response to overstory, site, seedbed and seed harvesting. Australian Journal of Ecology 19:96-102.

> Stoneman G L, Dell B & Turner N C 1994 Mortality of *Eucalyptus marginata* (jarrah) seedlings in Mediterranean-climate forest in response to overstorey, site, seedbed, fertilizer application and grazing. Australian Journal of Ecology 19:103-109.

Surveys of the burrowing bettong (*Bettongia lesueur*) by J Short and B Turner, of the CSIRO Division of Wildlife and Ecology, Midland, on Bernier, Dorre, Barrow and Boodie Islands of Western Australia, confirmed their being widespread and abundant on the first three islands, but not on Boodie Island. The burrowing bettong has been extinct on the mainland since the early 1960's, and is now restricted to <0.01% of its formerly natural range.

> Short J & Turner B 1993 The distribution and abundance of the burrowing bettong (Marsupialia: Macropodoidea). Wildlife Research 20:525-534.

The diet of the noisy scrub-bird, a small, semi-flightless inhabitant of scrub and forest on the south coast of Western Australia, is described by A Danks (CALM, Two Peoples Bay Nature Reserve) and M Calver (Murdoch University). Adults and nestlings eat similar prey, but in differing proportions. Adults take mainly ants, beetles and spiders, whereas nestlings consume mainly spiders and crickets. It might be unrewarding for adults to transport small prey (ants), or heavily sclerotised prey (beetles), to the nestlings.

> Danks A & Calver M C 1993 Diet of the noisy scrub-bird *Atrichornis clamosus* at Two Peoples Bay, South-western Western Australia. Emu 93:203-206.

The history, distribution, present status, breeding, sociality, demography and management of the two subspecies of purple-crowned fairy-wren is described by I Rowley and E Russell (CSIRO Division of Wildlife and Ecology, Midland). These birds occupy very restricted riverine vegetation across the Wet-Dry tropics of northern Australia, between the 400 and 1000 mm isohyets. The less numerous Kimberleyan subspecies is separated from the more abundant Carpentarian subspecies by 200 km of unsuitable habitat. The territorial birds breed mainly in the dry season (March-September), in large nests usually located at the base of a *Pandanus aquaticus* leaf. Annual productivity from the clutch of 2-3 is about 1 yearling per group of parents and associated mature progeny that cooperatively raise the young.

> Rowley I 1993 The purple-crowned fairey-wren *Malurus coronatus*. I. History, distribution and present status. Emu 93:220-234.

> Rowley I & Russell E 1993 The purple-crowned fairey-wren *Malurus coronatus*. II. Breeding biology, social organisation, demography and management. Emu 93:235-250.

Hakea trifurcata, a dimorphic species of Proteacea, has two distinct leaf types (needle and broad), unlike other *Hakea*. The broad leaves, which superficially resemble the fruits and are located near them, are produced only by mature plants. Feeding trials by P Groom, B Lamont and H Duff, of Murdoch University, showed that the white-tailed black cockatoo

removed fewer fruits when broad leaves were present, indicating an unusual case of 'self-crypsis' wherein fruits mimicked the unrewarding broad leaves.

> Groom P K, Lamont B B & Duff H C 1994 Self-crypsis in *Hakea trifurcata* as an avian granivore deterrent. Functional Ecology 8:110-117.

Detailed information on the diet type and size of the Arafura filesnake, based on a 4-year field study, enabled D Houston and R Shine, of Sydney University, to demonstrate seasonal variation in diet that was also related to the size and sex of the filesnakes. Female snakes generally fed on a single, large prey whereas males consumed numerous, smaller prey.

> Houston D & Shine R 1993 Sexual dimorphism and niche divergence: Feeding habits of the Arafura filesnake. Journal of Animal Ecology 62:737-748.

A cooperative research study by researchers from the Agriculture Protection Board and Department of Agriculture, investigated the mobility of red kangaroos in arid Western Australia. The versatility in home range size, mobility, and dispersal of red kangaroos defies the conventional definitions of 'home range', and indicates the importance of irregular and temporary environmental dispersal in the behavioural repertoirs of this species.

> Norbury G L, Norbury D C & Oliver A J 1994 Facultative behaviour in unpredictable environments: Mobility of red kangaroos in arid Western Australia. Journal of Animal Ecology 63:410-418.

An interdisciplinary study by zoologists from the University of Western Australia and chemists from Murdoch University examined the role of urea and methylamines (TMAO, betaine, sarcosine) to the buoyancy of three western Australian elasmobranchs (whiskery shark, whaler shark and shovelnosed ray). Particularly urea and TMAO contribute significant positive buoyancy, and this must be considered as an additional adaptive advantage to the well-accepted roles of urea and TMAO as balancing osmolytes, and TMAO as a counteracting solute.

> Withers P C, Morrison G, Hefter G H & Pang T.-S. 1994 Role of urea and methylamines in buoyancy of elasmobranchs. Journal of experimental Biology 188:175-189.

The hypothesis that predation rate by snakes may select for nest spacing and winter breeding in New Holland honeyeaters was tested by researchers from the Australian Museum. Results supported the notion that clumped nests experienced greater predation by birds, but not that winter breeding may have evolved as a strategy to avoid predation by snakes.

> Major R E, Pyke G H, Christy M T, Gowing & Hill R S 1994 Can nest predation explain the timing of the breeding season and the pattern of nest dispersion of New Holland honeyeaters? Oikos 69:364-372.

Physical Sciences

Researchers from Murdoch University have shown using Mössbauer spectroscopy that nanoscale iron oxide particles inside the protein ferritin can be converted by treatment with hydrogen sulphide gas to a layered structure of iron oxide and iron sulphide within the protein shell. Coagulation of these particles is prevented by the hydrophobic protein casing.

> St. Pierre T G, Chua-anusorn W, Sipos P, Kron I & Webb J 1993 Reaction of hydrogen sulphide with native horse spleen ferritin. Inorganic Chemistry 32:4480-4482.

Polarised neutron diffraction experiments by B Figgis and P Reynolds, of the University of Western Australia, and J Cable, of Oak Ridge National Laboratory, USA, show that the bonding between technetium and chlorine in the ion $TcNCl_4^-$ is highly covalent. Their measurements demonstrate the covalence of transition-ligand bonds in a more direct way than previously possible.

Figgis B N, Reynolds P A & Cable J W 1993 Extreme covalence in the Tc-Cl bond from polarized neutron diffraction. Journal of Chemical Physics 98:7743-7745.

Physicists at the University of Western Australia have used a polarised photon coincidence experiment to study the state multipoles and the partial cross sections for the excitation of helium atoms by an electron beam. Their results provide stringent tests for existing theories of collision processes, which are shown to be only in qualitative agreement with the experimental data.

Mikosza A G, Hippler R, Wang J B & Williams J F 1993 Determination of rank 4 multipoles and of partial cross sections for the He(3 ^{1}D) excitation by electron impact. Physical Review Letters 71:235-238.

Quantum mechanical calculations employing silane (Si_xH_y) molecules have been used by scientists at Murdoch University to model the electronic structure of hydrogenated amorphous silicon. Calculations of the valence band density of states were in excellent agreement with experimental Auger electron spectra. The results obtained confirm that disorder in silicon lattices increases the defect states in the valence band and that hydrogenation ties off the dangling bonds associated with the photodegradation of amorphous silicon.

Lund C P, Clare B W, Jennings P J, Cornish J C L & Hefter G T 1994 An experimental and theoretical study of Auger lineshapes in hydrogenated amorphous silicon structures. Surface Science 303:266-276.

Note from the Hon Editor: This column helps to link the various disciplines and inform others of the broad spectrum of achievements of WA scientists (or others writing about WA). Contributions to "Recent Advances in Science in Western Australia" are welcome, and may include papers that have caught your attention or that you believe may interest other scientists in Western Australia and abroad. They are usually papers refereed journals, or books, chapters and reviews. Abstracts from conference proceedings will not be accepted. Please submit short (2-3 sentence) summaries of recent papers, together with a copy of the title, abstract and authors' names and addresses, to the Hon Editor or a member of the Publications Committee: Dr S D Hopper (Life Sciences), Dr A E Cockbain (Earth Sciences), and Assoc Prof G Hefter (Physical Sciences). Final choice of articles is at the discretion of the Hon Editor.

"Letters to the Editor" concerning scientific issues of relevance to this journal are also published at the discretion of the Hon Editor. Please submit a word processing disk with letters and suggest potential reviewers or respondents to your letter. *P C Withers, Hon Editor, Journal of the Royal Society of WA.*

Convergent Evolution in the Dentitions of Grazing Macropodine Marsupials and the Grass-Eating Cercopithecine Primate *Theropithecus gelada*

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Abstract

This study examines the dentitions of two sets of non-ungulate grazers in relation to their diets. These sets were the grazing macropodine marsupials (including the genera *Macropus*, *Peradorcas*, *Onychogalea* and *Lagorchestes*) and the large, grass-eating cercopithecine primate *Theropithecus gelada*. The two sets are highly selective grazers whose diets consist mainly of green grass parts. Both were found to share four unusual dental adaptations for trituration of grasses and extension of the active life of the cheek teeth despite the severe abrasive effects of their diets: 1) bilophodont molars, which when worn present distinctive patterns of longitudinal and transverse enamel cutting ridges; 2) arrangement of the mandibular cheek teeth in an upwardly convex curve (reversed Curve of Spee) so that occlusion between these teeth and their maxillary counterparts is concentrated in a small anterior area of the tooth row instead of along its entire length; 3) accelerated anteriad movement of cheek teeth propelled by the anterior force of occlusion that permits relatively unworn, posterior elements of the cheek tooth battery to be moved anteriorly into areas of intensified function; and 4) enlargement of the transeptal interdental fibres of the periodontal ligament to maintain close contact between the elements of the cheek tooth row and thus convert the row into a single functional unit.

This convergent evolution of grazing macropodine marsupials and a grass-eating primate is particularly interesting because the adaptations for grazing are considered highly derived in both the macropodine and cercopithecine lineages, and that the pathway of evolutionary change followed similar courses in both groups. Adaptations for grass-eating are thought to have arisen in ancestral types of both lineages that subsisted on diets of softer, less resistant vegetation and that possessed dentitions that lacked specializations for the reduction of large quantities of abrasive, high-fibre vegetation and the preservation of relatively unworn tooth substance throughout adult life.

Introduction

Herbivores face considerable problems imposed by the high rate of wear on their teeth caused by mastication of large quantities of tough, fibrous and frequently abrasive vegetation. These problems are particularly serious in grazers, which consume large quantities of grasses that are rich in abrasives. Grasses contain endogenous abrasive silicates (phytoliths) that deter attack from herbivores, and potentially damaging exogenous abrasive materials such as sand and grit from soil. Many mammalian species have evolved various combinations of dental modifications to enlarge the surface area of the postcanine teeth, to prolong the life of these teeth, or both that compensate for the rapid rate of dental wear caused by these abrasive materials. Enlarging the total surface area of the cheek tooth permits better subdivision of plant material into small parts, although this requires increased muscular force. This increased subdivision facilitates either direct digestion of starch or indirect digestion of cellulose through microbial symbionts. A similar effect is gained by increasing the total length of the tooth's enamel cutting edges.

The strategies that have evolved in various mammalian lineages for the exploitation of grasses as a primary source of food are many and varied, with each grazing lineage possessing its own unique combination of features for harvesting, chewing and digesting grass parts. Because grass is low in simple sugars, low in protein and high in fibre, successful grazers must strike a balance between the metabolic energy they expend in processing grass and the energy they receive in return. The complex carbohydrates present in grasses cannot be directly metabolized by mammals, and so most grass-eating mammals have evolved modifications of their digestive tracts for fermentative breakdown of these carbohydrates into usable sugars and volatile (short-chain) fatty acids. The two basic styles of gut fermentation that have evolved in mammals, foregut fermentation and hindgut fermentation, differ in their efficiencies and have been incorporated in two rather divergent feeding strategies in the animals that use them. Foregut fermenters (*e.g.* artiodactyls, kangaroos, and colobine monkeys) extract high metabolic yields from moderate amounts of relatively high-quality forage, while hindgut fermenters (*e.g.* perissodactyls) rely on bulk feeding of lower-quality forage to compensate for a reduced nutrient extraction rate (Janis 1976). Accordingly,

the teeth of foregut fermenters tend to be somewhat simpler in design than those of hindgut fermenters because they are required to process less vegetation of generally higher quality (*i.e.* lower in fibre and abrasives, and higher in water content).

The mechanical properties of foods differ, with some requiring more compression or crushing and others (such as grasses) requiring more cutting or shearing. An optimal crush/shear ratio exists for breaking up each type of food (Osborn & Lumsden 1978), and the masticatory apparatus of every species has evolved, in part, to generate the crush/shear ratio best suited to its preferred diet. As discussed by Osborn (1993), this ratio depends on the direction of tooth movement during mastication, the orientation of the occlusal surfaces of the teeth and the direction of the bite force.

Feeding on grasses is usually related to the evolution of several specific dental modifications that are used in various combinations. The most common of these modifications include an extreme increase in the surface area of the teeth, the evolution of complex enamel patterns on the occlusal surfaces, an increase in the height of the crowns of the molars, and the conversion of the molars into rootless, continuously growing structures. Of these, the first two act more to increase the surface area and food-processing efficiency of the tooth while the last two act to prolong the life of the tooth. The high-crowned (hypsodont) molars of certain perissodactyls, artiodactyls and rodents, for example, are usually associated with an abrasive diet and are commonly assumed to have evolved in response to the consumption of abrasives associated with grasses (Stirton 1947; Janis & Fortelius 1988). Manatees (genus *Trichechus*), consumers of sea grasses, have evolved yet another strategy – that of continuous posterior eruption of an indefinite number of new molars in response to the wear and anterior shedding of the anterior molars (Domning & Hayek 1984).

Because the dentition is only one part of the grazer's digestive armament, it breaks down grasses in a manner that is complementary to the type of fermentation that will occur in the gut. On the basis of the rather limited number of major types of molar and jaw design we see in grazing mammals, however, there would appear to be design constraints that are operating on the evolution of these structures in specific lineages. Some of these constraints no doubt derive from the mechanical properties of the dental hard tissues themselves and the need to minimize the potential for crack propagation in brittle enamel (Koenigswald *et al.* 1987). In each grazing lineage, there is a unique compromise between the size of individual cheek teeth, the design of the occlusal surfaces of the teeth, the total number of cheek teeth an animal can develop in its life, and the number of teeth in occlusion at any one time. The anatomical compromise that evolves in any grazing lineage is teeth that must be powerful enough to physically break down grasses yet durable enough to last through the entirety of the animals' reproductive lives. Increasing the amount of tooth material (and therefore the area and total length of cutting edges) is one solution for increasing grass comminution and reducing wear. However, the cost of larger teeth to the animal, in the development of the teeth themselves, in larger masticatory muscles and in dental supporting tissues, is great. An enlarged masticatory apparatus is energetically costly to construct and maintain, and in some lineages the costs appear to outweigh the benefits.

Among mammals, neither herbivorous marsupials nor primates exhibit the extreme dental modifications for coping with high rates of dental wear seen in lineages with long evolutionary histories of grazing (*e.g.* perissodactyls or artiodactyls). Yet, among both the Metatheria and the Primates there are species that rely exclusively on diets of grasses. These species display unusual dental modifications that increase the efficiency of the postcanine teeth in the comminution of grasses and that prolong the life of the postcanine dental battery, but that differ from those of other more widely known grazers (Jablonski 1981). In this study, the dentitions of the grazing Australian macropodine marsupials comprising the genera *Macropus*, *Peradorcas*, *Onychogalea* and *Lagorchestes* and the large cercopithecine monkeys known as geladas or gelada baboons (*Theropithecus gelada*) of the highlands of central Ethiopia are examined. These groups have been compared because of the remarkable similarities observed in their postcanine dentitions. Similarities in diet and dental morphology between the grazing macropodines and the geladas are explored in detail. The evolutionary histories of these animals are then compared to see if the apparent convergence in dental structure and function between the groups can be related to similarities in selective pressures acting on similar ancestral morphologies in their respective lineages. .

Dental Structure and Function in Relation to Diet

Grazing Macropodines

Among the extant Macropodidae, species of *Macropus*, *Peradorcas*, *Onychogalea* and *Lagorchestes* have been classified as grazers because of their reliance on abrasive, high-fibre vegetation often in the form of grasses. Although some species-specific and regional variations in dietary preferences have been reported among these species, grasses dominate their diets (Jarman 1984). For instance, the diet of *Macropus giganteus* in southwestern Queensland is supplemented by dicotyledons throughout the year (Griffiths & Barker 1966, Griffiths *et al.* 1974), while that of *M. rufus* includes drought-resistant shrubs in dry times (Jarman 1984). Grazing macropodines are highly selective feeders, which can use their narrow muzzles and incisal arcades to pick individual grass blades. They show a preference for green, readily digestible material and avoid, where possible, highly fibrous and dry plant parts (Jarman 1984).

The structure and function of the teeth in grazing macropodines was described in detail by Sanson (1978, 1980), who defined a series of five characters associated with a diet of abrasive, high-fibre plants. These were: 1) bilophodont molars with strong links (longitudinal ridges) between the transverse loph(id)s; 2) a convexly curved lower tooth row (describing a reversed Curve of Spee) that meets the upper row at a tangent so that only the anterior portions of the tooth row are in occlusion; 3) occlusion that consists of an initial forward motion of the lower molars followed by a marked lateral movement in which the developed links are in contact with the opposing lophs; 4) molar progression, by which relatively unworn lower molars are advanced to anterior positions in the jaw while worn molars are shed anteriorly; and 5) reduced or vestigial permanent premolars.

A
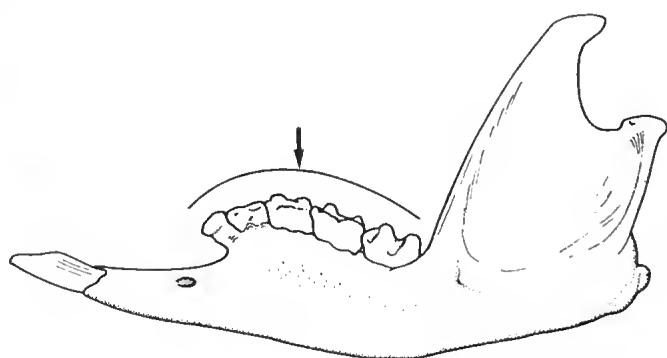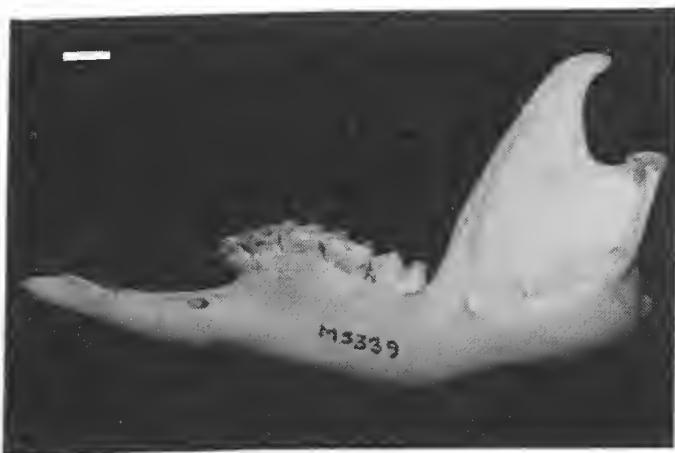
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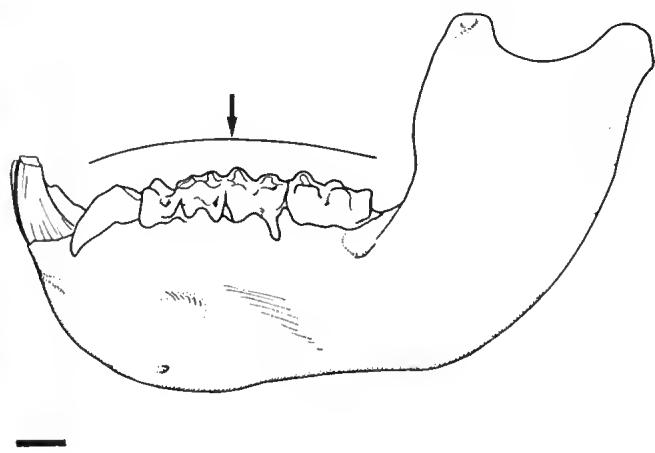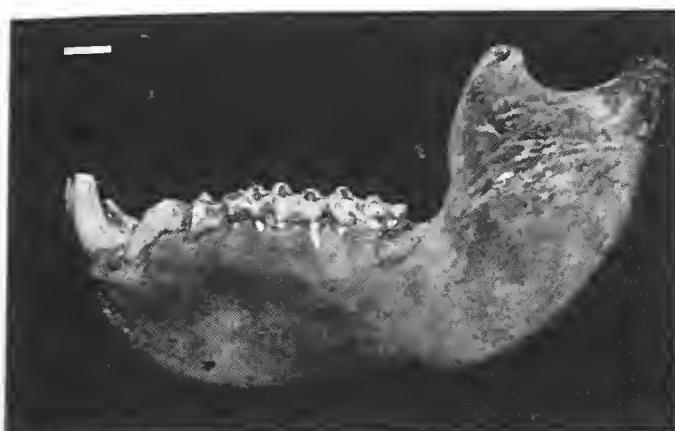
Figure 1. Comparison of the dentitions of a grazing macropodine (A; *Macropus robustus;* W.A. Museum M5339) and a grass-eating primate (B; *Theropithecus gelada* HKU / UWA 0242) in lateral view. In the line drawings of the same specimens, the curves represent the reversed Curves of Spee and the arrows indicate the regions of the dentitions at the most superior points on the curves where the forces of mastication are most strongly concentrated. Scale bars in all views indicate one centimeter.

These basic anatomical characteristics of the dentition of grazing macropodines are illustrated in Fig 1A and Fig 2A. The Curve of Spee is a term used to describe the upwardly concave profile of the human mandibular dentition as viewed from the side. A reversed Curve of Spee is an upwardly convex curve of the lower dentition.

As described by Sanson (1980), mastication in grazing macropodines is ideally suited to the comminution of tough, fibrous materials. Processing of plant materials is accomplished mostly by cutting on the sharp enamel edges of the molar teeth. Although the sharpest cutting edges are on unworn molars, further cutting edges are exposed as the enamel on the surface of the crown wears and the underlying dentine is exposed and excavated (Fig 2A). The efficiency of the molar increases up to a certain point, after which the molar is so worn that it is no longer effective as a cutting tool. Because the focus of cutting action is at the point of contact between two enamel cutting surfaces, the wearing down of those surfaces will result in diffusion of occlusal pressure over a larger area and less effective comminution (Sanson 1980).

As their functional life approaches an end, molars move into nonfunctional positions in the anterior portion of the jaws before being shed. Through the process of molar progression, a molar tooth erupting in the mandible moves anteriorly and dorsally into the occlusal plane. The molar continues to move anteriorly and dorsally as it becomes worn and, at the height of its functional life, occupies a position on the most superior point on the reversed Curve of Spee (Figure 1). As the tooth wears further, molar progression moves it anteriorly and ventrally out of the occlusal plane until it is shed (Sanson 1980). This process begins with shedding of the premolars and their position in the jaw being taken by the first molar, with the other erupted molars following. Molar progression continues with the wearing down and shedding of the first, second and subsequent molars in succession (Tyndale-Biscoe 1973). The process of molar progression appears to be driven by the direction of the force of occlusion. Anteriad movement of the mandibular dentition relative to the maxillary dentition during mastication produces anteriorly directed forces that, in turn, are transmitted to the dentition as a whole by the transeptal interdental fibres of the periodontal ligament (Sanson & Miller 1979). These fibres act as links in a chain to maintain tooth-to-tooth contact. Normally, in kangaroos, only four molars erupt in each jaw so that very old individuals may have only one worn molar tooth left in each jaw. Thus, the
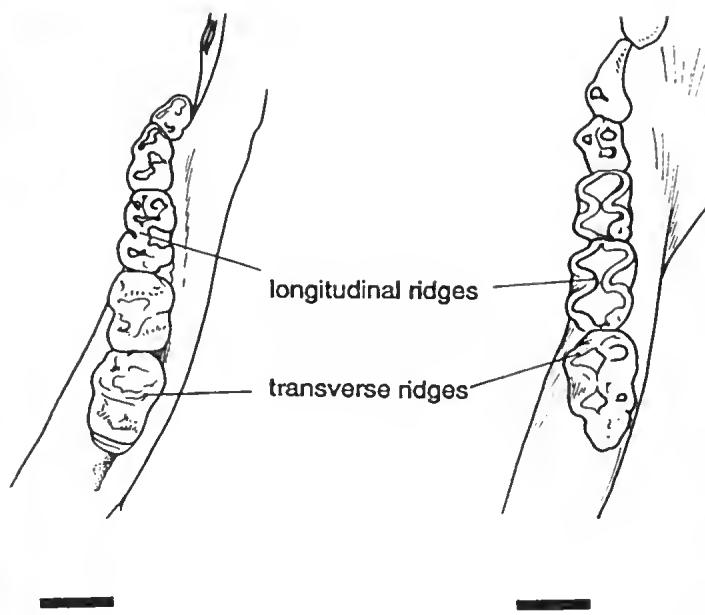
Figure 2. Cheek teeth of a grazing macropodine (*Macropus robustus*) and a grass-eating primate (*Theropithecus gelada*) in occlusal view (specimens as in Fig 1). Line drawings of the same specimen indicate the transverse and longitudinal enamel ridges that shear against their counterparts in the upper dentition to comminute grass parts during mastication. Scale bars in all views indicate one centimeter.

life span of these animals is dictated in large part by the durability of their teeth. Only in the little rock wallaby, *Peradorcas concinna*, are new molars continuously produced in the back of the jaws, apparently in response to a diet of grasses and ferns that are rich in abrasive silica (Sanson *et al.* 1985).

Theropithecus gelada

Among Primates, *Theropithecus gelada* is unique in its almost exclusive reliance on a diet of grasses. Geladas prefer grass blades to herbs or shrub vegetation when the former is available (see Iwamoto 1993a for a review). In the localities where the feeding behaviour of geladas has been observed throughout the year, grasses were found to constitute 90% of the diet in the wet season, but around 60% at the height of the dry season. Although green grass blades constitute most of the grass parts eaten, grass seeds are intensively exploited by geladas when they are available. Geladas are highly selective feeders but, unlike grazing macropodines which crop grass with their incisors, they harvest young grass blades between the highly opposable first and second digits of the manus before transferring them to the mouth. The same technique is used for the harvesting of rhizomes, which form an important part of the diet in the dry season (Iwamoto 1993a). Because geladas do not clean the rhizomes before ingestion, this increases their consumption of exogenous abrasives from the soil. Feeding is generally a continuous operation in which the animal masticates the previous handful of grass parts while gathering the next (Dunbar 1977). The time geladas spend feeding each day is longer in the dry season than in the wet season because the animals must spend longer to find green blades and succulent stem bases of grasses (Iwamoto 1993a, b). The ability of geladas to harvest vegetation quickly and with great precision appears to have been an ancient attribute of the *Theropithecus* lineage,

as judged by the fact that the digital proportions of the gelada were presaged in a Pliocene member of the lineage (Jablonski 1986).

In *T. gelada*, the demands of mastication of an abrasive, high-fibre diet are met with a series of structural modifications of the teeth and jaws that make possible particularly efficient trituration of large quantities of grass parts (Jolly 1972, Jablonski 1981, 1993a). In the dentition, these modifications comprise five major features: 1) bilophodont molars with columnar cusps that, when worn, present a pattern of complexly curved enamel cutting ridges; 2) alignment of the mandibular cheek teeth in a reversed Curve of Spee so that, for much of the life of the individual, contact between the upper and lower tooth cheek tooth rows is concentrated anteriorly; 3) occlusion that is characterized by a short anteriad movement followed by a marked lateral component that permits the transversely and longitudinally oriented enamel cutting edges in the lower cheek tooth row to move across those of the upper row; 4) accelerated mesial drift of the molar teeth promoted by heavy interproximal wear and delayed eruption of the lower third molars, by which relatively unworn molars are moved to more functional, anterior positions in the jaws; and 5) possession of enlarged mesial shelves and distal accessory cuspules on the first and second permanent molars, and a large and consistently well-formed hypoconulid on the lower third molars in order to increase the functional length of the cheek tooth rows (Jolly 1972; Jablonski 1981, 1993a; Swindler & Beynon 1993). The basic anatomical characteristics of the dentition of *T. gelada* are illustrated in Fig 1B and Fig 2B.

The molars of the gelada display considerably more occlusal relief at most wear stages than do those of any other cercopithecines, but they probably approach optimum operational efficiency in a relatively unworn state when the

greatest number of exposed enamel ridges is available for separation of plant material (Jablonski 1981; Meikle 1977). In unworn molar teeth, the cusp pairs of the mesial and distal loph(id)s are partly separated by deeply waisted buccal and lingual enamel folds. When worn, this arrangement produces a series of incomplete transverse ridges of harder enamel alternating with softer dentine (Fig 2B). Because of the height of the cusps of the molars and the depth of the clefts and basins, the molars of *T. gelada* retain occlusal features for a long time (Meikle 1977). Further, the long buccal surfaces of the molar teeth permit the long anatomical crown to function until the root supporting system of the teeth is compromised (Swindler & Beynon 1993).

In *T. gelada*, the highest occlusal pressures can be generated at an anterior position in the jaws, at the apex of the reversed Curve of Spee (Jablonski 1981; see Fig 1B). During the early part of adult life, this is where the upper and lower first permanent molars come into contact, but as these molars wear and move anteriorly in the jaws their positions are gradually occupied by the anterior loph(id)s of the second permanent molars, followed by the posterior loph(ids). The curved orientation of the lower tooth row, the action of mesial drift and the delayed eruption of the elongated lower third molar tooth help to ensure that relatively unworn tooth substance is retained until late in life (Jablonski 1981). In one mandibular specimen (HKU/UWA 0242), the fourth premolar showed severe wear of the interproximal enamel and a worn occlusal surface, the first molar was heavily worn on the occlusal surface while the second molar was only slightly so, and the large third molar was barely worn and the root apices were still open (Miller & Jablonski, unpublished observations). One of the effects of this process is the production of a steep wear gradient in the molars of *T. gelada*, characterized by considerably heavier wear in the anterior than the posterior molars at any given time (Jablonski 1981).

The mesial drift that occurs in the gelada is not the same as the molar progression in the grazing macropodines, in which the continual movement of molars is accommodated by sequential loss of anterior teeth. In *T. gelada*, all the molars are, generally, retained throughout life and are not shed, despite very heavy occlusal and interproximal wear. Near loss of anterior cheek teeth by shedding has only been observed in one aged female specimen, which interestingly, also possessed supernumerary upper fourth molars. In *T. gelada*, several features of the alveolar bone and periodontal ligament indicate that the cheek teeth are functioning and moving as a unit. These include the presence of buttressing bone around the mandibular cheek teeth and enlargement of the trans-septal interdental fibres of the periodontal ligament (Miller & Jablonski, unpublished observations). Anterior movement of the cheek teeth in the gelada appears to be driven, at least in part, by the anterior force of occlusion, but marked anterior movement (and shedding of obsolescent teeth anteriorly) seems to be prevented by the stabilizing effect of the large upper canine and lower sectorial premolar (Miller & Jablonski, unpublished observations).

Evolution of Dental Form and Function

The similarities in dental morphology shared between grazing macropodines and geladas are striking, despite major differences between the two groups in overall cranial shape. Both groups possess bilophodont molars which, while different in the cusp and crest disposition in the unworn state, appear remarkably similar when moderately worn. The sequence of dentine and enamel ridge exposures produced by interproximal (interdental) wear and wear on the occlusal surfaces is virtually identical in both groups, although it appears that the more bunodont macropodine molars approach functional obsolescence earlier than those of the gelada.

The similarities between the groups in the conformation and movement of the cheek teeth in the jaws are perhaps even more remarkable than those of the teeth themselves, and distinguish them from their respective non-grazing relatives. In both groups, the reversed Curve of Spee acts to concentrate the muscular force exerted by the muscles of mastication in a relatively small, anteriorly located area of the tooth row. Molar progression in the macropodines and mesial drift in the geladas provide mechanisms by which animals of both groups are provided with a continuous supply of relatively unworn and highly efficient triturating surfaces to this focal point of occlusal pressure. The geladas' adaptation is the more conservative because heavily worn molars are retained in the jaws, resulting in an eventual flattening of the occlusal profile in old age and apparent dispersion of the force produced by the muscles of mastication over a larger area of the molar row. Anteriad movement of molars continues throughout life in the gelada, but the continuous, slot-machine-like replacement of molars at the back of the jaws does not occur as it does in grazing macropodines or, as it does in the even more extreme form, in the manatee and *Peradorcas*. In this regard the geladas can be viewed as lying at the conservative end of a spectrum of dental and gnathic adaptations common in non-ungulate grazing mammals to extend the active life of the cheek teeth despite the severe abrasive effects of diet.

Discussion

Morphologists are quick to identify "adaptive features" in the animals they study, but it is difficult to prove or establish the adaptedness of these features without resorting to circular argumentation. Reference to conditions in an "outgroup" is a method that reduces circularity and, in the case of the animals under consideration here, the adaptedness of the dental morphology in one group is supported by that discovered in the other distantly related group. As Davis stated, "the convergent appearance of similar conditions in more or less remotely related organisms under similar or identical environmental conditions is the most readily available proof of adaptive value" (1949, p. 80).

The identification of a similar suite of dental characteristics in two phyletically distant lineages argues strongly in favour of the occurrence of convergent evolution of dental form and function in response to closely comparable environmental stimuli in the two lineages. Further, this demonstration of convergence argues strongly for the adaptive advantage of the unusual suite of features of the dentitions of the two lineages in relation to graminivory.

Sanson (1978) has argued that macropodines belonging to the "derived grazing grade" can be contrasted to those of the "ancestral browsing grade". Those macropodines he

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assigned to the browsing grade (*e.g. Wallabia, Dorcopsis, Dendrolagus* and *Setonix*) subsist on diets of relatively non-abrasive vegetation of low fibre content, such as the leaves of dicotyledonous plants, and occasional fruit and flowers. Their dentitions lack the conspicuous adaptations for the processing of tough vegetation and the preservation of tooth substance, and instead are characterized by bilophodont molars with weak longitudinal ridges, a flat cheek tooth row in which the permanent premolar and the four molars in the upper and lower jaws meet each other along a flat occlusal plane, and modest amounts of mesial drift (Sanson 1978). The derived grazing grade of macropodines evolved from the ancestral browsing grade, Sanson (1978) reasoned, as a response to climatic and ecological events beginning in the terminal Miocene that spurred the decline of mesic vegetation in the central regions of Australia and the rise of xeric grasslands.

The specialized nature of the dentition of *Theropithecus* has been recognized for many years and, as in the case of the grazing macropodine dentition, is a relatively recent innovation that can ultimately be traced to late Tertiary climatic and ecological change. Although some aspects of the emergence of the genus are still not fully understood (see Jablonski 1993b), the *Theropithecus* dentition clearly represents a highly derived condition for the tribe comprising the largest cercopithecines, the Papionini. The dentitions of other papionins such as macaques (*Macaca*) and common baboons (*Papio*) more closely resemble the primitive condition for the tribe in the absence of conspicuous adaptations for exclusive graminivory. Compared with the molars of *Theropithecus*, their molars possess more bunodont crowns with shallow notches and clefts and are arrayed in a flat tooth row. Moderate levels of molar wear in these animals result in the exposure of a simpler pattern of exposed enamel and dentine on the occlusal surfaces and the production of a more even wear gradient along the cheek tooth row.

The emergence and early diversification of *Theropithecus* in the Pliocene in East Africa was clearly linked to the evolution of a feeding apparatus specialized for the eating of grasses (Jablonski 1981, 1993a). This made possible the invasion of the more open, grassland environments that were evolving in East Africa in the late Miocene. The specializations for grazing in *Theropithecus* included those of the hand — that permitted early theropiths to harvest the vegetation of the emergent grassland environments — and those of the masticatory apparatus (Jablonski 1986, 1993a). *Theropithecus* thus occupies a position in what could be called the derived grazing grade for primates.

The dental specializations in both the grazing macropodines and the geladas represent apparent compromises between the demands of diet and constraints of dental and gnathic design in the two lineages. In both, the total length of the enamel shearing crests and cutting edges of the molars has been increased relative to that seen in their browsing counterparts (Benefit & McCrossin 1990) and, at least in the case of the geladas, it can be argued that these features could not have been increased further within the constraints of a bilophodont tooth. In addition, both lineages — with their reversed Curves of Spee and mechanisms of molar progression or mesial drift — have evolved similar, simple mechanisms for conserving relatively unworn occlusal surfaces long into adult life while maximizing the occlu-

sal pressures that can be exerted between opposing molar teeth. The reversed Curve of Spee concentrates occlusal pressures in a small area of the cheek tooth row and thus helps the animals make the most of molars that, by the standards of grazing ungulates, are relatively simple. It would thus appear that the constellation of dental features shared by grazing macropodines and geladas constitutes an alternative "blueprint" for facing the adaptive challenges of graminivory. This suggestion is supported by the fact that the bilophodont lower molars of manatees, which are consumers of sea grasses, are also arranged in a reversed Curve of Spee and also are shed and replaced through molar progression.

The many parallels between the diets and dental anatomies of the grazing macropodines and the geladas still leave us with the question of why the dentitions of these distant lineages evolved in such remarkably similar fashions. Both groups represent ungulate-like grazers in non-ungulate orders and so have evolved their dental specializations in lineages that lack the more established, long-term anatomical commitments to grazing seen in perissodactyl and artiodactyl lineages. The basic pattern of bilophodonty seen in the molars of both groups under consideration is itself thought to be a modification that evolved to facilitate the processing of vegetation. Bilophodont molars were well established within the Macropodidae and Cercopithecidae by Middle Miocene times or, possibly, earlier (Benefit 1987; Hume *et al.* 1989) and thus must be considered as ancient elements of their anatomies. The fact that the evolution of grazing adaptations in the dentitions of both lineages took very similar courses would tend to suggest that the basic template of bilophodonty in both lineages was the product of a rigid developmental pattern that acted to limit or constrain architectural possibilities within the dentitions of both groups (Janis & Fortelius 1988). Such constraints may have seriously limited the potential anatomical responses to selective pressures in both lineages. As Janis & Fortelius (1988) noted, the evolution of hypsodonty — an increase in the height of the cusps of the teeth — is not a response to the pressure of increased wear that appears to be available to animals with bilophondont dentitions. The relatively few modifications of the molars that appear to have been possible in the animals under consideration were augmented by modifications of the supporting tissues to accentuate the food processing capabilities of the teeth while preserving relatively unworn tooth substance far into adult life. Selective feeding behaviour emerges as critical to the grazing adaptations of both groups, especially *T. gelada*, because of the lack of potential for generation of new tooth material once the adult ration has been exhausted.

In herbivorous mammals, the methods for mechanical breakdown of vegetation must complement those involved in chemical digestion, and both methods are clearly related to the metabolic rate of the animal under consideration. It is thus appropriate to consider how these parameters compare between the grazing macropodines and *Theropithecus*. As marsupials, grazing macropodines have lower metabolic rates than most placental mammals (McNab 1980). Their method of foregut fermentation permits them to break down the complex carbohydrates in cell walls, and their bilophodont molars serve the important function of chewing the food very finely in order to increase the surface area for microbial attack. Empirical determinations of basal metabolic rate in

geladas have not been performed, but evidence from the study of comparative brain volumes in cercopithecids suggests that their basal metabolic rate is low relative to closely related taxa of comparable body size (Martin 1993). Geladas are able to digest more than 50% of the crude fibre in their diet and appear to possess a hindgut microbial fauna for the fermentation of fibre (Iwamoto 1993b). Because of the limited capacity of geladas to digest the components of plant cell walls, their bilophodont molars must work to expose the contents of the cells by rupturing, as well as to finely comminute cell walls in preparation for microbial attack in the hindgut. Geladas are similar to ungulate hindgut fermenters in the ability to physically divide fibrous vegetation in the oral cavity, but they are less efficient at extracting protein (Dunbar & Bose 1991). In the dry season, when the nutritional value of grasses declines because of desiccation, geladas increase their grass intake, but supplement their diet with large volumes of the succulent herb *Trifolium* (Iwamoto 1993b). That geladas do not engage in the same degree of bulk feeding on grasses in the dry season as do ungulate hindgut fermenters reflects their limited ability to extract protein from this source.

When estimated metabolic requirements are taken into account, grazing macropodines and geladas appear to have similar compromises in their modes of physical and chemical breakdown of vegetation. The macropodines can satisfy their relatively low energy requirements and protein needs through the relatively slow and thorough chemical digestion of very finely divided grasses in the foregut. Geladas satisfy their higher energy requirements and protein needs by high-volume intake and fine physical reduction of consistently high-quality vegetation. This is followed by relatively fast "bulk processing" in the gut that involves only partial fermentation of ingesta in the hindgut.

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Re-examination of the Murchison Downs meteorite:
A fragment of the Dalgaranga mesosiderite?

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Abstract

The Murchison Downs mesosiderite was reportedly recovered in 1925 from a locality *ca.* 200 km to the NE of the crater- forming Dalgaranga mesosiderite in Western Australia. A comparison of data from the literature on the chemistry and mineralogy of Murchison Downs and Dalgaranga, and a re-investigation of the metallography and mineralogy of Murchison Downs and Dalgaranga, suggests strongly that the two meteorites belong to the same fall. Murchison Downs may be one of the few examples of a meteorite transported by Aborigines and, pending further work, should be paired with the Dalgaranga meteorite.

Introduction

Meteorites have been recovered throughout Western Australia over the last century. Currently, specimens from 141 distinct meteorites have been documented from the State, representing more than 50% of all meteorites known from Australia (Bevan 1992). Conventionally, meteorites take the name of the geographical locality where they fell or were found. 'Paired' meteorites are those suggested, because of geographical propinquity and classification, to belong to a single fall (Hey 1966). However, when two or more meteorites were found at different times and allocated different names, but were subsequently proved conclusively to be from the same fall or find, then they are said to be 'synonymous' and the name of the meteorite first recovered usually takes precedence. Conversely, meteorites thought to be from the same fall are sometimes found on further examination to be distinct. For these reasons, the number of distinct meteorites known from Western Australia has fluctuated in the past without necessarily any addition of new material.

The Murchison Downs meteorite (Western Australian Museum registration number WAM 12586), a small metallic slug weighing 33.5 grams (Figure 1), was found in 1925 and described briefly by Simpson (1927), who noted that an etched surface of the meteorite displayed a Widmanstätten pattern and classified the meteorite as an iron with a fine octahedral (Of) structure (*e.g.* see Graham *et al.* 1985). Recently, Wasson *et al.* (1989) have provided a modern analysis of the Murchison Downs meteorite showing that it is a metallic nodule from a mesosiderite. In this paper, metallographic, mineralogical and chemical data are pre-

sented suggesting that the Murchison Downs meteorite is probably a transported fragment of the Dalgaranga mesosiderite.
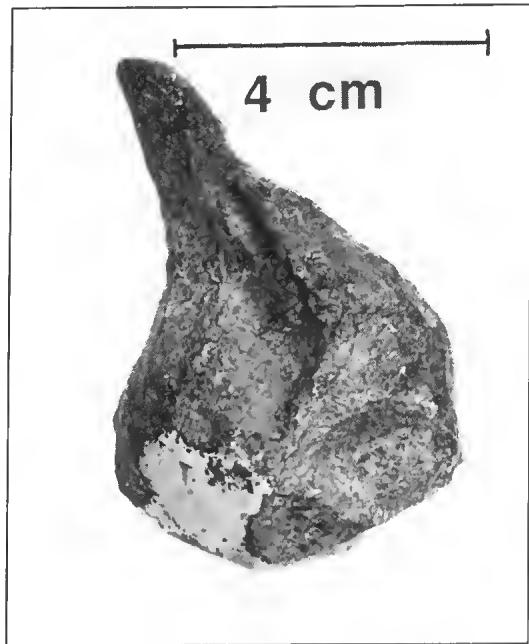
Figure 1. The Murchison Downs meteorite (Western Australian Museum number 12586).

Recovery and historical details

Few details of the discovery of the Murchison Downs meteorite are known. Neither the exact locality, nor the name of the finder was recorded. In the Annual Report of the Geological Survey of Western Australia for 1925, Gibb Maitland records the find-site as Murchison Downs Station

in the Kyarra district of the Murchison Division and notes the 'donor' of the specimen (GSWA 1/3894) as "Richardson". Simpson (1927) records the co-ordinates of the find-site as approximately 26° 40'S, 119° 0'E which correspond to a site close to 'North Cattle Well', situated *ca.* 15 km north of the homestead on 'Murchison Downs' Station and approximately 200 km to the north-east of the Dalgaranga crater. Since Simpson's (1927) observations were made, no detailed metallographic description of the meteorite has been published. However, McCall and de Laeter (1965) noted that the Murchison Downs meteorite "was similar to the small twisted irons commonly found near meteorite craters."

In contrast, the discovery of the Dalgaranga crater and recovery of its associated meteorites are well documented. This small crater, measuring 25 m in diameter, was discovered in 1923 by G E P Wellard at co-ordinates 27° 43'S, 117° 15'E on Dalgaranga Station, north of Yalgoo (Simpson 1938). Wellard is reported to have recovered a large number of meteorite fragments from the vicinity of the crater but the repository of this material is unknown. Simpson (1938) described a metallic fragment of the Dalgaranga meteorite weighing 42 grams, which he classified as a medium (Om) octahedrite.

In 1959, and again in 1960, H H Nininger and G I Huss of the American Meteorite Laboratory visited the Dalgaranga crater and from the surrounding plain collected 207 specimens with an aggregate weight of 1098 grams. In addition,

they recovered 280 specimens, weighing approximately 9.1 kg, of deeply weathered material buried beneath the crater floor (Nininger & Huss 1960). Most of the specimens from the plain around the crater weighed individually less than 5 grams, and the largest weighed 57 grams. The material comprises both metallic and achondritic stony portions and the classification of the meteorite as a mesosiderite by Nininger & Huss (1960) was later confirmed by McCall (1965).

Metallographic, mineralogical and chemical details

A metallographic examination (this work) of an etched section (1.5 x 1.5 cm) of the Murchison Downs meteorite (WAM 12586—formerly Geological Survey of Western Australia Collection 1/3894) reveals that this meteorite consists predominantly of plates of α-Fe,Ni (kamacite), γ-Fe,Ni (taenite), γ'-Fe,Ni (tetrataenite) and $\alpha + \gamma$ Fe,Ni (plessite) in octahedral arrangement. On two perpendicular sections, the bandwidths of plates of kamacite (excluding those in plessite) vary from 0.3-0.5 mm with a mean of 0.45±0.1 mm. This kamacite bandwidth lies within the 'fine octahedrite' group of the modern structural classification of iron meteorites (Buchwald 1975). Troilite and schreibersite occur as irregular inclusions, and several small (mm-sized) inclusions of non-metallic minerals composed of low-Ca orthopyroxene (Fs$_{34}$), anorthitic plagioclase feldspar (An$_{91}$),

Table 1
Electron microprobe analyses of non-metallic minerals in the Murchison Downs and Dalgaranga meteorites.
Analysts: B J Griffin and G D Pooley. - indicates not detected

	Murchison Downs			Dalgaranga	
	orthopyroxene	plagioclase	chromite	chromite	range[a]
SiO$_2$	52.7	46.2	-	-	
TiO$_2$	0.32	-	1.20	1.32	0.18-1.32
Al$_2$O$_3$	0.69	34.3	10.8	13.5	13.0-14.3
Cr$_2$O$_3$	-	-	54.6	52.0	51.3-52.41
V$_2$O$_3$	-	-	0.54	0.52	0.47-0.62
FeO[b]	21.1	-	28.6	28.2	27.0-28.2
MnO	0.83	-	1.74	1.60	1.50-1.88
MgO	22.6	-	2.70	3.54	3.42-4.19
CaO	1.80	18.4	-	-	
Na$_2$O	-	0.93	-	-	
K$_2$O	-	0.00	-	-	
Totals	100.04	99.83	100.18	100.68	

Molecular %

	Fs$_{34}$	An$_{91.6}$	ulvospinel	3.1	3.3
	En$_{62.4}$	Ab$_{8.4}$	spinel	21.9	26.8
	Wo$_{3.6}$	Or$_{0.0}$	chromite	74.3	69.1
			magnetite	0.7	0.7
		100Cr/(Cr+Al)		77.2	72.0
		100Fe/(Fe+Mg)		85.6	81.7

[a]range based on six analyses. [b]All Fe reported as FeO.

Al-rich chromite and a silica polymorph occur throughout the section. These inclusions are swathed with bands of kamacite up to 1.0 mm thick. Electron microprobe analyses of the non-metallic minerals in the Murchison Downs meteorite are given in Table 1.

The Widmanstätten pattern displayed by the Murchison Downs meteorite is not continuous; in addition to swathing kamacite around silicate inclusions, in the section examined a thick (1.00 mm) band of swathing kamacite partly bounds the external surface of the meteorite. Locally, the Widmanstätten structure displays moderate to severe mechanical deformation and kamacite and taenite plates are bent and kneaded. Kamacite is shock-hardened, displaying the cross-hatched ε-kamacite structure and abundant Neumann bands. Narrow zones of shear deformation occur in the metallic micro-structure of the meteorite along which fine scale (<1 µm) recrystallization has taken place. Under crossed polars, troilite displays abundant shock-twins and, where inclusions are traversed by shear zones, troilite has been recrystallized.

Table 2

Summary of the mineralogy of the Murchison Downs and Dalgaranga mesosiderites
(mineral compositions determined by electron microprobe analyser unless otherwise stated - indicates not recorded)

	Murchison Downs		Dalgaranga			
	Wasson *et al.* (1989)	This work	Hassanzadeh *et al.* (1990)	McCall (1965)	Nehru *et al.* (1980)	This work
silicates						
olivine	-	-	-	Fa_{13} [a]	$Fa_{13.38}$	-
orthopyroxene	$Fs_{25}En_{73}Wo_2$	$Fs_{34}En_{62.4}Wo_{3.6}$	present	Fs_{34} [b]	-	-
plagioclase	$An_{90\pm1}Ab_{9\pm1}$	$An_{91.6}Ab_{8.4}$	anorthite	$An_{72}Ab_{28}$ [b]	-	-
silica polymorph	present	present	-	-	-	present
metallic minerals						
kamacite (mm bandwidth)	(0.5)	(0.45±0.1)	$Fe_{93.6}Ni_{5.8}Co_{0.53}$ (0.3±0.1)	-	-	present
taenite	present	present	present	-	-	present
tetrataenite	present	present	$Fe_{48.3}Ni_{51.6}Co_{0.09}$	-	-	present
other minerals						
troilite	present	present	present	present	-	present
chromite	present	$Usp_{3.1}Sp_{21.9}Chr_{74.3}Mt_{0.7}$	present (Al-rich)	present	-	$Usp_{3.3}Sp_{26.8}Chr_{69.1}Mt_{0.7}$
schreibersite	present	present	present	-	-	present
cohenite	-	present	-	-	-	present

[a] determined by X-ray diffraction; [b] determined optically.

The Dalgaranga meteorite has been described by Nininger & Huss (1960) and McCall (1965). The material consists of disrupted fragments of mesosiderite; individual specimens ranging from nodules formed almost entirely of metal, through mixtures of metal and silicate, to essentially basaltic achondritic material. Nininger & Huss (1960) noted that those fragments composed mainly of metal are polycrystalline and display Widmanstätten patterns ranging from coarsest (Ogg) to finest (Off) octahedrite. The structures of many of these metallic slugs show extensive gross mechanical deformation and localised thermal altera-tion of the type often encountered in crater-forming iron meteorites. Other fragments show few signs of the effects of impact shock-metamorphism (Nininger & Huss 1960). Hassanzadeh *et al.* (1990) have described a metallic slug from the Dalgaranga meteorite and note the presence of clumps of silicates that comprise low-Ca pyroxene, anorthite, accessory troilite, schreibersite and an Al-rich chromite.

Published mineralogical data for both Murchison Downs and Dalgaranga meteorites (and those determined in this work) are summarised in Table 2. Simpson (1938), Wasson

Table 3

Summary of published analyses of metal in the Murchison Downs and Dalgaranga mesosiderites

	Ni (%)	Co (%)	Ga µg/g	Ge µg/g	Ir µg/g	Cr µg/g	Cu µg/g	As µg/g	Sb ng/g	W ng/g	Re ng/g	Pt µg/g	Au µg/g
Murchison Downs[1]	9.16	0.49	13.6	56.1	4.98	221	144	12.5	310	1110	600	8.9	1.32
Dalgaranga [2]	10.27	0.48	12.7	-	4.99	12	172	11.9	260	990	600	8.0	1.37
Dalgaranga [3]	8.8	-	15.5	56.0	4.2	-	-	-	-	-	-	-	-
Dalgaranga [4]	8.63	-	-	-	-	-	-	-	-	-	-	-	-

[1] Wasson *et al.* (1989); [2] Hassanzadeh *et al.* (1990); [3] Wasson *et al.* (1974); [4] Simpson (1938)

et al. (1974) and Hassanzadeh *et al.* (1990) have analysed the metal in the Dalgaranga meteorite, and their data, compared with those of Wasson *et al.* (1989) for the Murchison Downs meteorite, are shown in Table 3

Discussion

Excluding olivine, the silicate mineralogy of both the Dalgaranga and Murchison Downs meteorites consists essentially of low-Ca orthopyroxene and anorthite. Accessory minerals in both meteorites include troilite, schreibersite and an Al-rich chromite. In the Murchison Downs meteorite, Wasson *et al.* (1989) reported a fine-grained silica polymorph, probably tridymite, which is confirmed in this work. In the Dalgaranga meteorite, olivine with the range of compositions Fo_{87-62} Fa_{13-38} (Nehru *et al.* 1980), generally occurs as nodules and phenocrysts in the stony portions of the meteorite (McCall 1965). Olivine has not been found in the Murchison Downs meteorite. However, in mesosiderites, olivine is only rarely associated with metallic nodules. Additionally, tridymite has yet to be reported from the Dalgaranga meteorite, although Hassanzadeh *et al.* (1990) note that it is a sub-group 'A' mesosiderite that are known to be tridymite-rich (Hewins 1984). Nevertheless, the mineral compositions of those silicates in the Dalgaranga and Murchison Downs meteorites that have been analysed by modern methods are generally very similar (Table 1). The composition of the pyroxene (Fs_{34}) reported in this work for the Murchison Downs meteorite is identical to that reported for the Dalgaranga meteorite by McCall (1965). While this differs from the pyroxene composition (Fs_{25}) reported for the Murchison Downs meteorite by Hassanzadeh *et al.* (1990), Powell (1971) has shown that pyroxene compositions within individual mesosiderites can be highly variable, though rarely falling outside the range Fs_{20-40}. The compositions of grains of plagioclase can also be variable ranging from An_{80} to An_{98}. McCall (1965) reports an optical determination of plagioclase in the Dalgaranga meteorite with the composition $An_{72}Ab_{28}$ (bytownite) that is very different from analysed plagioclase reported for the Murchison Downs meteorite (Wasson *et al.* 1989; see Table 2), but is also different from the 'anorthite' reported for the Dalgaranga meteorite by Hassandazeh *et al.* (1990).

In contrast to silicates, Powell (1971) and Bunch & Keil (1971) noted that there is generally little compositional variability in chromite for a given mesosiderite. Major oxides in chromite rarely vary by more than 13% of the amounts present, with TiO_2 being the most variable component. Variations in the composition of chromite (notably Al and Mg) between the Murchison Downs and Dalgaranga meteorites are greater than one would normally expect from a single meteorite. However, chromite compositions within fragments of the Dalgaranga meteorite are similarly variable. One grain of chromite associated with a serpentine-group mineral in a weathered portion of the Dalgaranga meteorite showed extreme TiO_2 depletion and MgO and Al_2O_3 enrichment that may be attributed to alteration during severe terrestrial weathering. Simpson (1927) noted one small grain of cohenite in the Murchison Downs meteorite which is confirmed in this work. Minor amounts of cohenite also occur in the Dalgaranga meteorite.

The reported bulk Ni contents of metal in the Dalgaranga meteorite (Table 3) vary from 8.63 %wt (Simpson 1938) to 10.27 %wt (Hassanzadeh *et al.* 1990) consistent with the observed structural heterogeneity of the metallic portions of the meteorite. With the exception of Cr, there is a very close correspondence between the major, minor and trace element contents of metal in the Dalgaranga and Murchison Downs meteorites (Table 3). The Cr content of metal in the Murchison Downs meteorite (221 µg/g) reported by Wasson *et al.* (1989) is 18.5 times greater than that reported by Hassanzadeh *et al.* (1990) for the Dalgaranga meteorite (12 µg/g). This is outside the usual variation in replicate analyses of the same meteorite and could indicate that the two meteorites are distinct. However, it is possible that the high Cr content of the Murchison Downs meteorite reported by Wasson *et al.* (1989) is due to the presence of microscopic inclusions of chromite in the small sample of metal (off WAM 12586) that was analysed (J T Wasson, *pers. comm.*).

On the basis of cluster analysis for a number of elements, notably Ni and Au, in metallic nodules from twelve mesosiderites, Hassanzadeh *et al.* (1990) recognised various sub-groups of mesosiderites. Eight closely related clusters are recognised, and three moderately related clusters are designated low-AuNi, high-AuNi and intermediate-AuNi. Significantly, the Murchison Downs and Dalgaranga meteorites, along with the South Australian mesosiderite, Pinnaroo, form one closely related cluster belonging to the high-AuNi sub-group of mesosiderites (Hassanzadeh *et al.* 1990).

Structurally, the thick band of swathing kamacite that bounds a portion of the exterior surface of the Murchison Downs meteorite is typical of the heterogenous nucleation of this mineral encountered in the metallic nodules from mesosiderites, and indicates that the metal originally formed in contact with either silicates, or some other non-metallic phase. The deformed and locally heat-altered nature of the metallographic structure of Murchison Downs is characteristic of meteorites that have been involved in a crater-forming impact. The style and extent of thermo-mechanical alteration displayed by the Murchison Downs meteorite is identical to that in many of the metallic slugs of the Dalgaranga meteorite. To date, no young meteorite impact crater other than the Dalgaranga crater has been identified in the immediate vicinity of Murchison Downs Station or elsewhere in the Murchison Division of Western Australia.

Summary and Conclusions

The data presented in this paper confirm the re-classification by Wasson *et al.* (1989) of the Murchison Downs meteorite as a mesosiderite but are insufficient to prove, conclusively, that it is a fragment of the Dalgaranga mesosiderite. Notwithstanding, there is little evidence to suggest that they are from different falls. The distance between the find-sites of Dalgaranga and Murchison Downs (*ca.* 200 km) would normally preclude pairing. Mesosiderites are extremely rare and account for less than 1% of all known meteorites. Remarkably, two other mesosiderites (Mount Padbury and Pennyweight) have also been found in the same general area as the Dalgaranga and Murchison Downs meteorites. The suggestion by Mason & Jarosewich (1973) that the Mount

Padbury and Dalgaranga meteorites may be fragments of the same meteorite has been shown by Wasson *et al.* (1974) to be highly unlikely. Also, Hassandazeh *et al.* (1990) show that the Pennyweight and Murchison Downs mesosiderites belong to the low- and high-AuNi sub-groups, respectively, and are probably distinct. However, the discovery in the same general area of two mesosiderites (Dalgaranga and Murchison Downs) that have been involved in crater-forming impact militates against their being from separate falls.

There are a number of explanations as to how the Murchison Downs fragment could have became displaced from the vicinity of the Dalgaranga crater. One possibility is that the Murchison Downs fragment became detached during atmospheric passage of the impacting projectile. However, if this was the case, then the meteorite would not show evidence of damage due to large scale, explosive impact. Moreover, the small size of the Dalgaranga crater (25 m in diameter) makes it very unlikely that the fragment could have been thrown 200 km by the impact event. The most likely explanation is that the fragment was transported by human agency. This could have occurred at any time prior to the discovery of the Murchison Downs meteorite in 1925. The age of the Dalgaranga crater is variably reported from 3000 years (Shoemaker & Shoemaker 1988) to around 25,000 years (Nininger & Huss 1960; Grieve 1991). These ages lie well within the accepted time of Aboriginal occupation of Australia (40,000 years) and it is possible that the impact of the Dalgaranga meteorite was witnessed by Aborigines. Although Aborigines were not known to have collected or utilized meteoritic iron, it is possible that the Murchison Downs meteorite is one of the few examples that have been transported by Aborigines. Pending further work, it is suggested that Murchison Downs be paired with Dalgaranga.

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Invertebrate community structure related to physico-chemical parameters of permanent lakes of the south coast of Western Australia

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Abstract

The aquatic invertebrate fauna and a range of physical and chemical parameters were recorded in twenty-three permanent lakes within 20 km of the coast between Cape Naturaliste and Albany, Western Australia. Invertebrates were collected by qualitative sweeps, benthic cores and plankton trawls to sample all major habitats. A total of 209 invertebrate taxa were recorded, representing a rich faunal diversity. Multivariate analyses showed that invertebrate community structure was most closely associated with salinity and nutrient status of the lakes; however, all salinities were below the limnologically accepted 3 g l⁻¹ upper limit for freshwater (Bayly & Williams 1973). Human activities are most likely responsible for the elevated nutrient levels recorded in some of the lakes.

Introduction

Lentic wetlands in the south-west of Australia, particularly lakes on the Swan Coastal Plain associated with urban development, have recently been the focus of much research. Wetlands on the Swan Coastal Plain today represent only about 30% of wetlands present prior to European settlement (Halse 1989) and many are now eutrophic due to urbanization and agriculture (Davis & Rolls 1987; Balla & Davis 1993; Davis *et al.* 1993).

In contrast, the permanent lakes along the south coast are less disturbed and have received little attention. Limnological studies on south coast lentic wetlands have mainly been restricted to temporary systems (Bayly 1982, 1992a; Christensen 1982; Pusey & Edward 1990a,b) although two permanent pools were included in the latter study. Recently, a survey of aquatic invertebrates in three lakes in the Two Peoples Bay area (Storey *et al.* 1993) outlined a highly diverse invertebrate fauna, with possible biogeographic links to south-western Tasmania. Establishing a database of physical, chemical and biological parameters in south-coast wetlands is essential for developing management procedures to deal with the impact of increased human activity. This study elucidates relationships between environmental parameters and invertebrate community structure for the lakes surveyed, and provides a database to assess the conservation value of the lakes to enable formulation of future management programmes.

Materials and Methods

Study sites

Twenty-three permanent lakes in the south of Western Australia were studied, all located on Vacant Crown Land within 20 km of the coast between Cape Naturaliste and Albany (Fig 1). Several of the lakes were not officially named and are therefore referred to as follows; the lake near the junction of Charley and Dunes Roads, Pemberton is Charley Lake; the lake north east of Windy Harbour is Windy Harbour Lake; for the group of lakes near Boat Harbour Road, Denmark, the eastern lake is Boat Harbour Lake 1, the western lake is Boat Harbour Lake 3 and the northern lake is Boat Harbour Lake 4.

Sampling regime

Fifteen lakes were sampled in 1991 during winter (25 June–2 July) and six of these, located across the geographical range of the survey, were re-sampled in spring (4–13 November), together with six additional lakes. Charley Lake and Lake Williams were sampled in early summer (18 & 19 December) because of forest quarantine restrictions; these were considered spring samples because typical hot/dry summer conditions had not commenced.

Environmental parameters

The physical and chemical parameters measured in the lakes, and the methods used are summarised in Table 1. Surface area of the lakes was estimated from enlarged photocopies of 1:50000 maps, using a Delta-T™ Area Meter. Temperature, dissolved oxygen and pH were measured from surface waters at each lake between 1030 and 1430 h. Depth was recorded along at least two transects for those lakes accessible to a boat. At these lakes, vertical profiles of dissolved oxygen and temperature were recorded to determine the extent of any stratification. The ratio of surface to bottom readings for temperature and dissolved oxygen was used as a measure of stratification in subsequent statistical analyses, where a ratio of one indicated no stratification.

Undisturbed water samples were taken for analyses for colour, turbidity, anions and cations. Salinity was calculated as the total concentration of the major cations (Mg, Ca, K and Na) and chloride in solution. These ions account for approximately 95% of the total soluble salts (TSS) for drainage basins
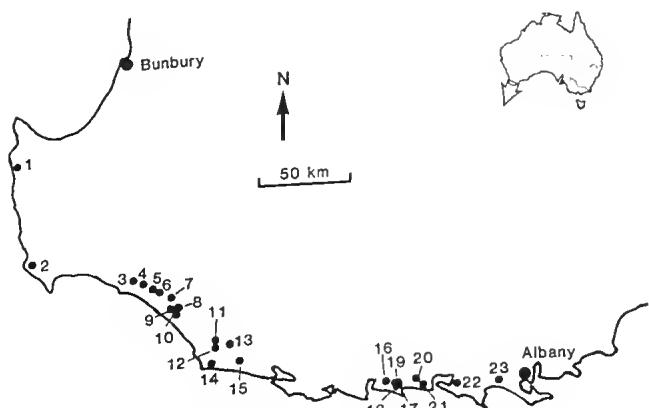
Figure 1. Map of locations of the lakes.

1. Quininup Lake	33 45' 48" S	115 00' 06" E
2. Lake Davies	34 13' 20" S	115 01' 58" E
3. Lake Quitjup	34 22' 58" S	115 35' 40" E
4. Lake Jasper	34 24' 40" S	115 40' 59" E
5. Lake Wilson	34 25' 39" S	115 43' 00" E
6. Lake Smith	34 25' 45" S	115 43' 26" E
7. Charley Lake	34 30' 21" S	115 49' 28" E
8. Yeagarup Lake	34 32' 43" S	115 52' 14" E
9. Neanup Lake	34 32' 47" S	115 51' 32" E
10. South Yeagarup Lake	34 33' 08" S	115 51' 58" E
11. Doggerup Lake	34 43' 03" S	116 03' 36" E
12. Lake Samuel	34 43' 55" S	116 03' 26" E
13. Lake Florence	34 44' 03" S	116 05' 57" E
14. Windy Harbour Lake	34 50' 00" S	116 02' 25" E
15. Lake Maringup	34 50' 00" S	116 11' 55" E
16. Owingup Lake	34 59' 56" S	117 03' 57" E
17. Boat Harbour Lake 1	35 01' 01" S	117 05' 59" E
18. Boat Harbour Lake 3	35 01' 01" S	117 05' 17" E
19. Boat Harbour Lake 4	35 00' 53" S	117 05' 46" E
20. Lake 12046	34 59' 56" S	117 13' 23" E
21. Lake Williams	35 01' 00" S	117 16' 03" E
22. Lake Saide	35 02' 34" S	117 28' 24" E
23. Lake Powell	35 01' 14" S	117 44' 16" E

on the south coast of Western Australia (Loh *et al.* 1983). Water samples for total nitrogen and phosphorus determinations were filtered in the field through a 0.22 μm Millipore™ filter using a 50 ml syringe. Samples for chlorophyll (a) determinations were taken by filtering a measured volume (approx. 1 l) of water through a Whatman™ GF/C filter, and the retained cells, containing chlorophyll, were stabilized with a few drops of a saturated magnesium carbonate solution. The filter was folded, blotted between gauze swabs and placed in a plastic bag on ice, out of the light, before being stored frozen in the laboratory. Chlorophyll (a) was then measured using the method described in Strickland & Parsons (1968). At each lake, a 10 cm deep core-sample of the benthic material was collected in a vertical-sided vial with 13.2 cm² lid opening. In the laboratory, the percent organic content was determined after drying at 40 °C and ashing in a muffle furnace at 450 °C for approximately eight hours.

Invertebrates

The methodologies for collecting fauna were designed to sample the major aquatic habitats and maximise the number of species recorded from each lake. Six random replicate benthic samples were taken with a 72 cm² core sampler to 10 cm depth from each lake. Samples were immediately preserved in 5% formalin. In the laboratory, the organic fraction was separated from the sediment by water elutriation and washed through a 250 μm sieve. The fauna was removed from the organic fraction using a dissecting microscope. All individuals were identified to the lowest taxon possible, usually species, either by the use of keys or by matching specimens to a voucher collection at the Aquatic Research Laboratory, Department of Zoology, The University of Western Australia. The Calanoida, Ostracoda and Cladocera

Table 1

Environmental parameters, methods of measurement and units of precision.

Parameter	Method / Apparatus	Precision	Acronym
Lake surface area	Estimated from 1:50000 map		SA
Temperature	Mercury thermometer & Yeo-Kal 602 Hamon salinity/temperature bridge	0.5°C 0.5°C	Temp
Dissolved oxygen	Nester portable meter	0.1 mg l⁻¹	DO
pH	Kane-May KM 7001 portable pH meter	0.1 pH unit	pH
Depth	Graduated line	0.05 m	Depth
Colour	UV-VIS spectrophotometer	5 APHA units	Col
Turbidity	Nephelometric method	0.1 NTU	Turb
Anions & cations	Atomic absorption spectrophotometer	0.4 mg l⁻¹	chemical symbols
Salinity	Sum of anion & cation concentrations		Sal
Total nitrogen	Auto analyser	0.01 mg l⁻¹	N
Total phosphorus	Auto analyser	0.01 mg l⁻¹	P
Chlorophyll (a)	Spectrophotometer	0.01 μg l⁻¹	Chloro
Benthic organic matter	Gravimetric method	0.01%	BOM

were forwarded to specialist taxonomists for identification. We include within *Calamoecia tasmanica* (Smith) *s.l.* the two forms *C. tasmanica* and *C. tasmanica subattenuata* described from Western Australia (Bayly 1992b). An estimate of abundance for each species was made according to the following categories; < 50 (rare), 50–500 (common) and > 500 (abundant) individuals.

A standard Freshwater Biological Association (FBA) D-net with 110 μm mesh was used to collect two-minute qualitative sweep samples from the substrate and amongst the macrophytes from the littoral margin of each lake. Samples were preserved in 5% formalin. In the laboratory, the fauna was removed from the organic matter in the samples, identified and categorised as for the benthic samples.

Plankton was sampled with a 110 μm mesh net, attached to a standard FBA D-net frame, held just below the water surface. Two samples were taken from each lake, using a standardised 50 m trawl for biomass determination and a shorter trawl for identification of the plankton species. Each sample was preserved in 5% formalin. Biomass was determined after drying the samples to constant weight at 40 °C. The taxa were identified and abundance categories estimated as for the benthic samples.

Data analyses

Multivariate analyses are useful techniques to outline patterns in complex biological phenomena (Gauch 1982) and these patterns are generally correlated to underlying environmental gradients (Wright *et al.* 1984; Furse *et al.* 1984; Moss *et al.* 1987). Principal components analysis (PCA) was used to ordinate the pattern of co-occurrence of the physical, chemical and morphological parameters measured for the lakes. This technique was used to reduce the complex data-set to a few, underlying 'factors' and to eliminate redundancies inherent in the data (Noruss 1986). This analysis was performed using the SPSS/PC⁺ advanced statistics procedure 'FACTOR'.

The total species information from each lake was classified by a polythetic divisive multivariate technique (Two-Way INdicator SPecies ANalysis; TWINSPAN, Hill 1979a). Subsequent groupings formed by TWINSPAN were correlated to environmental parameters by Multiple Discriminant Analysis (MDA; Noruss 1986) using the SPSS/PC⁺ version DSCRIMINANT. This analysis was performed between each TWINSPAN division. DEtrended CORrespondence ANAlysis (DECORANA, Hill 1979b) was used to ordinate the lakes on the basis of invertebrate community structure. DECORANA orders samples along an axis of similarity, where the lakes closest together on each axis have a more similar invertebrate community structure than those further apart.

Results

Environmental parameters

The 23 lakes studied ranged in surface area from 0.13 ha (Quininup Lake) to over 400 ha (Lake Jasper), with the majority of the lakes less than 100 ha in surface area (Table 2). The deepest lakes were Yeagarup and Jasper, both over 10 m (Table 2). Most of the lakes with larger surface area were shallow, ranging between about 0.8 m and about 1.3 m for Lake Powell and Owingup Swamp respectively.

Water colour was highly variable between lakes, ranging from < 5 APHA units at Quininup Lake to 740 APHA units at Lake Williams. The lakes were visually classified in this study as clear, brown and black corresponding to three APHA unit categories where clear is < 100, brown 100–300 and black > 300 (Table 3).

The pH ranged from 4.4 at Lake Florence to 8.6 at Lake Davies (Table 2). The values for pH were highly negatively correlated with colour (correlation coefficient r = -0.83, n = 29, p < 0.001). The low pH values probably reflected high humic/tannic content of darker waters (Table 3). The majority of these dark-water lakes lie on acid peat flats, a source of humic material. Lake colour was also correlated with water temperature (r = 0.51, n = 29, p < 0.01), probably due to dark water absorbing more solar radiation than clear water. Water temperatures between lakes ranged from 9.2–15°C in winter to 12.3–24°C in spring (Table 2). Temperature stratification (Table 2), with colder hypolimnetic water, which is the normal condition for deep water lakes, was recorded in Charley and Yeagarup Lakes in spring. In contrast, lakes Maringup and Jasper were stratified in winter, with warmer hypolimnetic water, which was interpreted as heating of the bottom sediments and hypolimnetic water by solar radiation in these clear-water lakes.

Salinity categories for the lakes were based on the classification for potable surface water by the Water Authority of Western Australia (1989a). The majority of the lakes were fresh; however Boat Harbour Lake 3, Lake Saide and Lake Powell were classified as marginal and Lake Davies and Owingup Swamp as brackish (Table 3).

On the basis of nutrient status (Wetzel 1975) Windy Harbour, Williams, Saide and Powell, were classified as eutrophic (Table 3). The other lakes were either oligo-mesotrophic or meso-eutrophic. Lakes sampled in winter usually had higher levels of phosphorus, probably from run-off of winter rainfall, elevating them into the meso-eutrophic category. The typical ratio of total nitrogen to total phosphorus (N:P) within the tissue of aquatic algae and macrophytes is 7:1 (Wetzel 1975). In Quininup Lake, Lake Smith, Neanup Swamp, and Boat Harbour Lake 3, the N:P ratios in the water were greater than 70:1 and therefore phosphorus was more likely the limiting nutrient. In contrast, for Lake Williams and, in winter, Lake Powell, the ratio was less than 4:1, indicating that nitrogen was the more probable limiting nutrient.

Turbidity measured in nephelometric turbidity units (NTU) ranged widely (Table 3), showing no obvious association with individual lakes. Turbidity and chlorophyll (a) were correlated (r = 0.61, n = 29, p < 0.01); high turbidity probably reflected the abundance of algal cells. Values for chlorophyll (a) ranged from 0.19 μg l⁻¹ in Yeagarup in late spring to 14.41 μg l⁻¹ in Lake Saide in winter (Table 3). Lower values for chlorophyll (a) were consistently recorded during spring. Based on the classification of Wetzel (1975) using chlorophyll (a) levels, the trophic status of most of the lakes was classified as oligotrophic and only lakes Powell, Saide, 12046, Boat Harbour 1, Boat Harbour 4, Windy Harbour and Owingup Swamp were classified as meso-eutrophic.

Benthic organic matter ranged from 0.16% in Lake Wilson to 87% in Boat Harbour Lake 1 (Table 3). The wide range reflects both differences in the nature of the catchments and

Table 2

Environmental information collected for each lake/occasion. W = winter, S = spring, ** = not recorded.

Lake	Season	SA (km²)	Max. depth (m)	Temp surface (°C)	Temp ratio[1]	DO surface (mg l⁻¹)	DO ratio[1]	pH (mg l⁻¹)	Na (mg l⁻¹)	K (mg l⁻¹)	Ca (mg l⁻¹)	Mg (mg l⁻¹)	Cl (mg l⁻¹)	Cation Dominance
Quininup Lake	S	0.0013	**	18.0	1	**	1	8.30	131.73	4.3	48.50	17.01	200.65	Na >Ca > Mg > K
Lake Davies	W	0.0116	4.3	13.1	1	11.1	1.12	8.64	474.74	11.7	30.46	84.56	814.64	Na > Mg >Ca > K
Lake Davies	S	0.0116	4.5	17.0	1	11.4	1	8.60	424.86	9.8	32.46	78.25	720.70	Na > Mg >Ca > K
Lake Quitjup	W	0.7261	1.4	12.2	1	12.4	1	7.53	70.81	1.6	1.60	6.80	113.79	Na > Mg >Ca = K
Lake Jasper	W	4.3751	10.1	10.7	0.88	12.5	2.78	7.52	67.59	2.1	8.42	6.32	107.41	Na > Ca >Mg > K
Lake Wilson	W	0.1731	1.7	12.0	1	12.5	1.19	5.55	51.73	1.2	1.20	4.62	84.02	Na > Mg >Ca = K
Lake Smith	W	0.0450	1.6	13.2	1	12.4	1	4.70	45.29	0.6	< 0.40	3.89	72.32	Na > Mg > K > Ca
Lake Smith	S	0.0450	1.6	16.0	1	11.1	1	4.50	31.27	0.7	< 0.40	2.67	48.92	Na > Mg > K> Ca
Charley Lake	S	0.0260	6.4	24.0	1.33	7.8	13.00	6.50	39.31	0.8	1.30	3.30	72.32	Na > Mg > Ca > K
Yeagarup Lake	W	0.1697	10.8	11.5	1	13.8	1	7.05	34.49	0.9	6.01	3.65	54.59	Na > Ca >Mg > K
Yeagarup Lake	S	0.1697	10.1	15.2	1.27	12.8	1	6.80	33.11	1.0	5.21	3.40	57.78	Na > Ca >Mg > K
Neanup Swamp	S	0.0833	**	16.0	1	**	1	6.40	34.71	1.1	8.02	2.92	54.24	Na > Ca >Mg > K
South Yeagarup Lake	S	0.0610	**	12.3	1	**	1	6.70	26.21	1.0	43.69	3.65	41.12	Ca > Na >Mg > K
Doggerup Lake	W	0.0831	**	10.8	1	12.3	1	**	34.26	1.1	< 0.40	3.40	52.82	Na > Mg > K> Ca
Doggerup Lake	S	0.0831	2.5	18.0	1	9.8	1	5.20	36.09	0.8	< 0.40	2.92	58.49	Na > Mg > K > Ca
Lake Samuel	S	0.0667	1.1	17.5	1	11.2	1	4.70	36.32	0.7	< 0.40	3.40	62.75	Na > Mg > K > Ca
Lake Florence	S	0.1044	1.5	18.0	1	10.4	1	4.40	35.40	0.9	< 0.40	2.92	51.76	Na > Mg > K> Ca
Windy Harbour Lake	W	0.0186	0.35	9.2	1	13.7	1	6.47	82.07	2.0	4.41	9.96	124.43	Na > Mg > Ca > K
Lake Maringup	W	1.3602	4.6	9.7	0.8	12.0	1	7.58	64.14	1.9	26.05	7.29	102.81	Na > Mg > Ca > K
Lake Maringup	S	1.3602	4.8	15.8	1	11.5	1	7.90	54.49	1.7	22.04	6.08	86.85	Na > Ca > Mg > K
Owingup Swamp	S	1.7886	1.3	19.5	1	11.2	1	7.40	340.48	1.5	17.64	58.08	717.15	Na > Mg > Ca > K
Boat Harbour Lake 1	W	0.2507	0.6	13.5	1	12.5	1	8.00	150.12	4.1	29.26	18.71	245.31	Na > Ca > Mg > K
Boat Harbour Lake 3	W	0.4235	0.8	14.5	1	12.2	2.09	8.10	241.40	6.2	48.10	27.70	407.32	Na > Ca > Mg > K
Boat Harbour Lake 4	W	0.1097	**	12.5	1	12.4	1	8.05	149.66	5.6	20.44	23.09	246.02	Na > Mg > Ca > K
Lake 12046	W	0.1014	4.9	10.3	1	12.9	1	7.70	182.31	16.9	22.04	16.77	250.63	Na > Ca > K > Mg
Lake Williams	S	0.0211	2.9	21.5	1	8.0	1.60	5.80	139.78	46.9	7.30	13.30	235.74	Na > K> Mg > Ca
Lake Saide	W	0.4125	1.1	13.0	1	12.7	1	8.40	150.35	6.6	99.80	22.60	245.31	Na > Ca > Mg > K
Lake Powell	W	1.3973	0.7	15.0	1	11.8	1	8.10	291.51	10.1	29.66	28.92	492.05	Na > Ca > Mg > K
Lake Powell	S	1.3973	0.9	19.0	1	11.0	1	7.10	211.05	6.2	25.25	22.36	363.72	Na > Ca > Mg > K

[1]Ratio of surface to bottom readings.

Table 3

Environmental information collected for each lake/occasion. W = winter, S = spring, * = below detection.

Lake	Season	Salinity (mg/1)	Salinity Category[1]	Colour (APHA units)	Colour classification[2]	Turb (NTU)	Chloro (a) (µg l⁻¹)	N (mg l⁻¹)	P (mg l⁻¹)	Trophic status[3]	BOM (%)
Quininup Lake	S	403	fresh	< 5	clear	0.3	0.58	5.80	< 0.01	oligo-mesotrophic	2.47
Lake Davies	W	1417	brackish	10	clear	0.4	0.64	1.10	0.01	meso-eutrophic	1.92
Lake Davies	S	126	brackish	10	clear	0.4	1.53	0.83	< 0.01	oligo-mesotrophic	1.29
Lake Quitjup	W	195	fresh	110	brown	0.9	0.42	0.56	0.01	meso-eutrophic	0.73
Lake Jasper	W	192	fresh	15	clear	0.8	2.56	0.69	0.01	meso-eutrophic	1.16
Lake Wilson	W	143	fresh	170	brown	0.7	1.07	0.46	0.02	meso-eutrophic	0.16
Lake Smith	W	122	fresh	380	black	0.4	0.43	0.70	0.01	meso-eutrophic	1.24
Lake Smith	S	84	fresh	530	black	0.9	0*	0.70	< 0.01	oligo-mesotrophic	3.44
Charley Lake	S	117	fresh	310	black	0.4	0.97	0.64	0.01	meso-eutrophic	11.25
Yeagarup Lake	W	100	fresh	180	brown	3.0	0.41	0.55	0.01	meso-eutrophic	3.62
Yeagarup Lake	S	91	fresh	260	brown	0.7	0.19	0.55	< 0.01	oligo-mesotrophic	2.24
Neanup Swamp	S	101	fresh	240	brown	0.8	0.80	0.73	< 0.01	oligo-mesotrophic	0.18
South Yeagarup Lake	S	116	fresh	100	brown	2.6	0*	0.43	< 0.01	oligo-mesotrophic	44.82
Doggerup Lake	W	92	fresh	300	black	0.4	0.53	0.52	0.01	meso-eutrophic	17.31
Doggerup Lake	S	99	fresh	330	black	0.4	0.20	0.55	0.01	meso-eutrophic	0.43
Lake Samuel	S	104	fresh	470	black	1.1	1.78	0.79	0.01	meso-eutrophic	66.04
Lake Florence	S	101	fresh	630	black	0.7	0.39	0.89	0.01	meso-eutrophic	1.42
Windy Harbour Lake	W	223	fresh	340	black	0.9	4.84	1.00	0.05	eutrophic	72.20
Lake Maringup	W	202	fresh	20	clear	0.3	0.62	0.61	0.01	meso-eutrophic	7.40
Lake Maringup	S	171	fresh	55	clear	0.3	0.40	0.48	< 0.01	oligo-mesotrophic	17.10
Owingup Swamp	S	113	brackish	220	brown	0.6	3.59	0.69	0.01	meso-eutrophic	0.61
Boat Harbour Lake 1	W	448	fresh	70	clear	0.4	3.24	0.92	0.01	meso-eutrophic	87.10
Boat Harbour Lake 3	W	731	marginal	20	clear	0.5	2.45	1.40	0.01	meso-eutrophic	43.82
Boat Harbour Lake 4	W	445	fresh	65	clear	0.6	4.82	0.83	0.01	meso-eutrophic	44.68
Lake 12046	W	489	fresh	110	brown	1.7	3.72	0.82	0.02	meso-eutrophic	46.42
Lake Williams	S	443	fresh	740	black	0.3	1.07	1.70	0.43	eutrophic	0.37
Lake Saide	W	525	marginal	80	clear	1.3	14.41	0.90	0.04	eutrophic	1.22
Lake Powell	W	852	marginal	220	brown	12.0	12.71	1.50	0.47	eutrophic	0.87
Lake Powell	S	629	marginal	190	brown	3.1	3.29	0.97	0.12	eutrophic	1.60

[1]Based on the Water Authority of Western Australia (1989a) classification for surface water; fresh = 500 mg l⁻¹ TSS, marginal = 500-1000 mg l⁻¹ TSS, brackish = 1000-5000 mg l⁻¹ TSS.

[2]Classification according to colour measurements in APHA units; < 100 = clear, 100-300 = brown, > 300 = black.

[3]Based on Wetzel (1975); oligo-mesotrophic = 5-10 µg l⁻¹ P & 250-600 µg l⁻¹ N, meso-eutrophic = 10-30 µg l⁻¹ P & 300-1100 µg l⁻¹ N, eutrophic = 30-100 µg l⁻¹ P & 500-15000 µg l⁻¹ N.

the patchy distribution of organic material within each lake as shown for the six re-sampled lakes (Table 3).

Factor analysis of the environmental data using principal components (PCA) indicated seven major factors (Table 4). The factors are numbered in decreasing amount of variation explained and therefore considered of decreasing 'importance'. Factor 1 showed the co-occurrence of depth with stratification and low nitrogen levels. Factor 2 showed co-occurrence of all cations and anions measured, except potassium, and salinity, illustrating that in the lakes with relatively elevated salinities, no single cation was responsible. Additionally, the lakes with elevated salinity had low colour. Factor 3 was a gradient generally of parameters that were different seasonally; temperature, dissolved oxygen and colour. Factor 4 showed the association of elevated phosphorus with chlorophyll and high turbidity (Table 4). Factor 5 showed that lakes with high pH, calcium, nitrogen and chlorophyll also had low colour levels. Factor 6 showed a gradient of nutrient levels (nitrogen, phosphorus and potassium) and colour. Factor 7 was a gradient of the

association of lake size with low levels of benthic organic matter. A total of 85.9% variation in environmental parameters was explained by these seven factors. The identification of these seven underlying factors greatly simplified the large data array, collapsing the information into co-occurring parameters. In subsequent analyses identifying gradients in the ordinations of invertebrate community structure, factors, rather than individual variables, were correlated with axes scores.

Invertebrates

A total of 209 taxa belonging to 6 phyla were recorded from the lakes, and the occurrence of the taxa in the lakes is shown in Appendix 1. The number of invertebrate species collected from each lake ranged from 18 in Lake Davies to 55 and 56 species in lakes Charley and South Yeagarup, respectively. Stepwise multiple regression analysis, with hierarchical inclusion of the number of species recorded in each lake against factor scores (Table 4), showed that Factors 2, 3 and 5 were significantly correlated ($p < 0.05$, F-value = 5.7,

Table 4

Factor scores calculated for the environmental variables and the percentage of variation explained by each Factor. A principal components analysis of the physico-chemical conditions associated with each site shows the pattern of co-occurrence of variables. The parameters highlighted in **bold** were considered 'significant', *i.e.* loading on any axis at > +0.30 or < -0.30 (Child 1970).

Parameter	F1	F2	F3	F4	F5	F6	F7
SA	0.163	0.007	-0.166	0.237	0.163	-0.247	**0.685**
Season	-0.134	-0.054	**0.916**	-0.153	-0.024	-0.026	0.034
Depth	**0.559**	-0.056	-0.154	**-0.302**	-0.014	0.245	**0.598**
Temp (surface)	0.106	0.100	**0.908**	-0.004	-0.003	0.201	0.057
Temp (bottom)	**0.900**	0.133	0.261	0.060	-0.032	0.103	0.151
Temp (ratio)	**0.945**	0.072	0.035	0.029	0.035	0.062	0.150
DO (surface)	**0.806**	0.117	**-0.425**	0.045	-0.268	-0.027	0.027
DO (bottom)	**0.871**	0.130	-0.183	0.094	0.058	-0.090	-0.120
DO (ratio)	**0.877**	0.014	0.122	0.012	0.079	-0.018	0.039
pH	**0.310**	0.225	0.161	0.097	**0.786**	-0.049	-0.026
Col	0.204	**-0.352**	**0.469**	0.123	**-0.584**	**0.336**	-0.196
Turb	-0.007	0.069	-0.045	**0.880**	0.024	0.017	0.154
Na	0.103	**0.963**	-0.022	0.117	0.155	0.119	0.027
K	0.100	0.253	0.105	0.172	-0.056	**0.824**	-0.097
Ca	-0.201	**0.335**	-0.170	0.213	**0.702**	0.072	-0.090
Mg	0.072	**0.981**	0.005	-0.037	0.117	0.025	0.017
Cl	0.110	**0.970**	0.026	0.116	0.125	0.073	0.049
Sal	0.093	**0.965**	0.002	0.121	0.169	0.107	0.030
Chloro	0.126	0.184	-0.249	**0.751**	**0.340**	0.041	-0.098
N	**-0.426**	0.063	0.131	-0.101	**0.475**	**0.553**	0.137
P	0.098	0.086	0.138	**0.735**	-0.126	**0.593**	0.082
BOM	0.032	-0.112	-0.293	-0.046	0.145	-0.071	**-0.735**
% variation explained	25.9	19.4	13.1	9.8	6.9	6.1	4.7

cumulative variation explained $r^2 = 0.41$). This indicated the importance of salinity, where lakes with lower salinities had higher species richness (Fig 2), and to a lesser extent, season, pH and nitrogen levels.
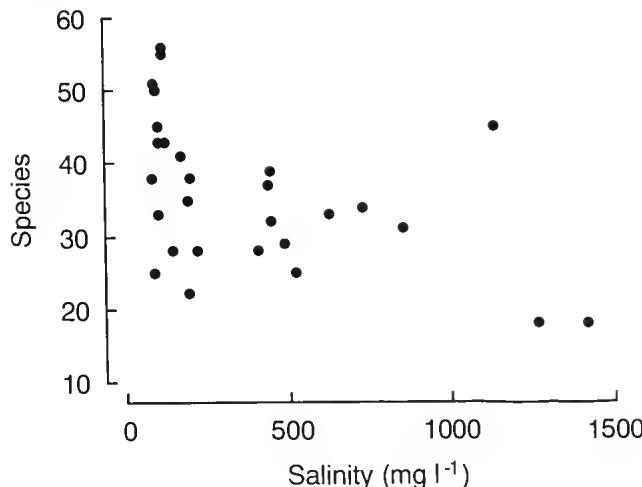
Figure 2. Regression analysis of total species richness *vs* salinity. The regression was significant $F_{(1,27)} = 7.63$, $p = 0.01$, $r = -0.47$, $n = 29$.

Zooplankton biomass was variable between lakes, ranging from zero in Doggerup Lake in winter to 678.5 mg in Lake Powell in winter (Appendix 1). The highest biomass values were recorded from lakes 12046 and Powell and consisted mainly of *Daphnia carinata* King.

TWINSPAN analysis of the total species data-set was taken to two levels and indicator species for each division are shown in Fig 3. The first and most important division

separated Powell, Quininup, Davies, Owingup, Boat Harbour 3 and Saide from the other lakes (division 1 and 2; Fig 3). This division was attributed primarily to salinity, based on the results of multiple discriminant analyses (Table 5). One TWINSPAN level two division separated lakes Saide and Powell from Quininup, Davies, Owingup and Boat Harbour 3 (division 3 and 4; Fig 3) and was associated with

Table 5

Discriminant analyses, using factor scores from PCA, on TWINSPAN (presence/absence) groupings. Discriminant analysis was performed at each TWINSPAN division, terminating at level two of the classification analysis. The table illustrates percent correct classification, the most important factors (entered stepwise) for discriminating between groups, and Wilk's Lambda. All significance levels shown were $p < 0.05$. The values in brackets indicate the direction of the correlation between factor scores and TWINSPAN groupings.

Groups	% correct	Variables	Interpretation	Lambda
1/2	100	F2	high salinity	0.46 (-)
		F5	high pH/nitrogen	0.32 (-)
		F4	high phosphorus	0.27 (-)
		F7	large size	0.23 (+)
3/4	100	F4	high phosphorus	0.36 (-)
		F2	high salinity	0.28 (+)
		F1	stratified	0.22 (+)
5/6	95	F5	high pH/nitrogen	0.63 (-)
		F1	stratified	0.37 (+)
		F3	high temperature	0.26 (+)
		F2	high salinity/low colour	0.23 (-)
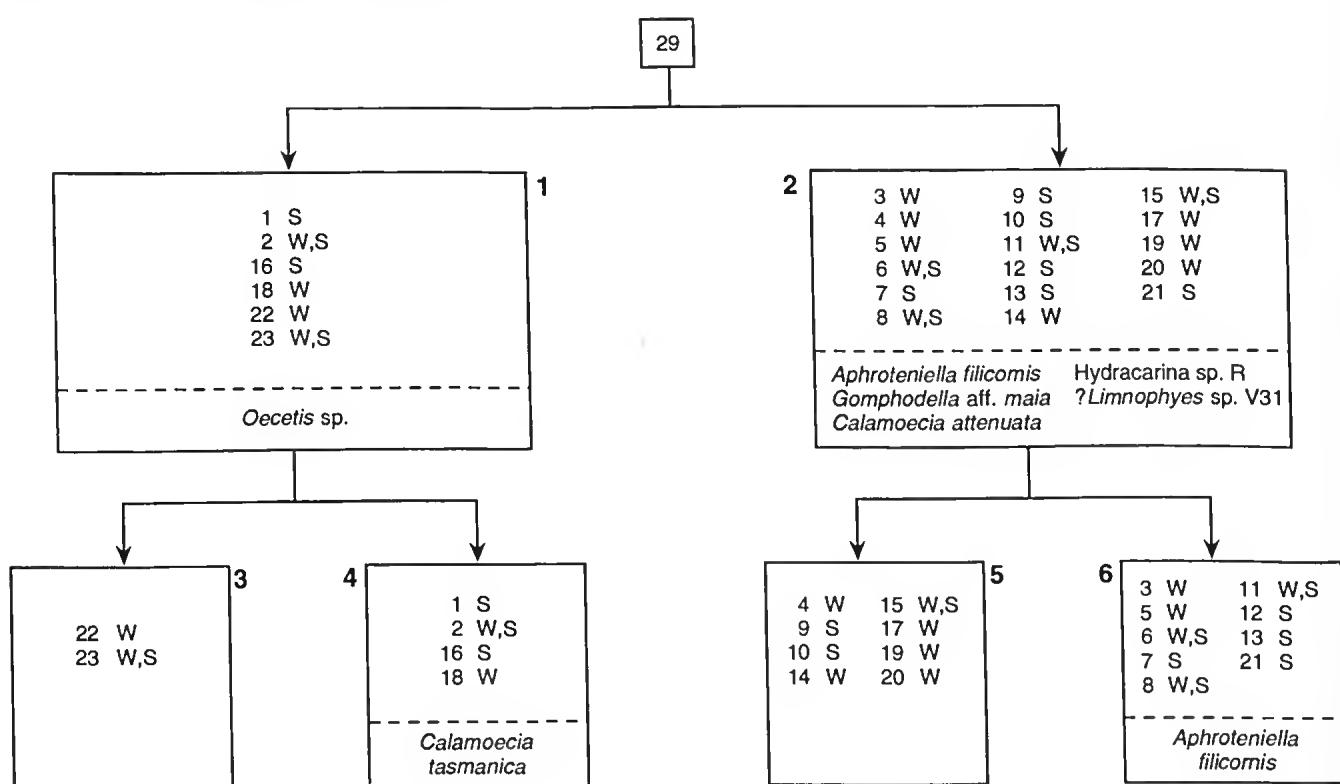
Figure 3. Dendrogram showing TWINSPAN classification of the lakes using the total species list. Indicator species are shown at the bottom of the boxes. Lake numbers as in Figure 1. W = winter, S = spring.

phosphorus levels (Table 5). The second level two division of other lakes (division 5 and 6; Fig 3) was associated with pH and nitrogen levels (Table 5).

Ordination by DECORANA on the total species data-set is presented in Figure 4. Along axis one, the obvious separation is of lakes Powell and Saide from the other lakes. Axis one was a gradient of pH, salinity and phosphorus concentration. These variables explained 32, 27 and 16% of the total respectively (Table 6).
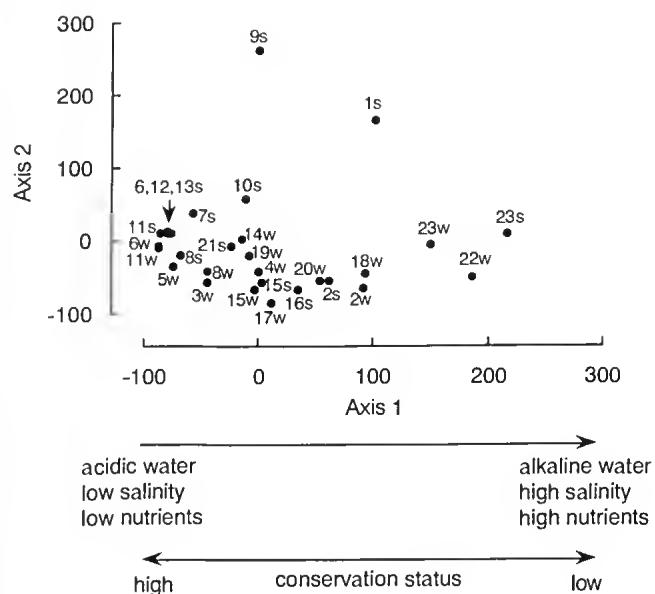
Figure 4. Axis 1 by axis 2 plot of DECORANA scores using total species for each lake. w = winter, s = spring. Lake numbers as in Figure 1.

Table 6

Results of stepwise multiple regression analysis, with hierarchical inclusion of DECORANA axes scores against environmental parameters. The cumulative variation explained (r^2) by each variable and F-values are presented. All factors where the F-values were significant at $p < 0.05$ are shown in the table.

Dependent variable	Factor	Interpretation	r^2	F-value
Axis 1 scores	F5	pH/nitrogen	0.32	12.6
	F2	salinity	0.59	18.8
	F4	phosphorus	0.76	25.8
Axis 2 scores	F1	depth/stratification	0.47	24.1
	F3	season	0.69	28.4

Discussion

The permanent lakes of the south coast of Western Australia contained a highly diverse invertebrate fauna, totalling 209 taxa. However, the total taxa count would have been higher if the Nematoda and Annelida could have been identified to species. An interesting feature of the fauna was the number of species that previously had been recorded in lotic habitats in Western Australia. Five of the dragonfly

species; *Austrogomphus lateralis* (Selys), *Hemigomphus armiger* (Tillyard), *Lathrocordulia metallica* (Tillyard), *Hesperocordulia berthoudi* (Tillyard) and *Synthemis cyanitincta* (Tillyard) are considered to be stream species (Watson 1962). Within the Chironomidae, 14 species; *Paramerina levidensis* (Skuse), *?Zavrelimyia* sp. V20, *Ablabesmyia* sp. V37, Orthocladiinae sp. V43, *Cricotopus annuliventris* (Skuse), *?Limnophyes* sp. V31, *Thienemanniella* sp. V19, *Dicrotendipes* sp. V47, *Nilothauma* sp., *Riethia* sp. V4, *Riethia* sp. V5, *Harnischia* sp. VCD10, *Stempellina ?australiensis* Freeman and *Aphroteniella filicornis* Brundin have been recorded only from upland streams of the jarrah and karri forests (Edward 1986; Storey & Edward 1989). The Trichoptera, except Leptoceridae sp. F, sp. H and sp. I, the Amphipoda *Perthia acutitelson* Straškraba and the Dytiscidae beetle *Sternopriscus browni* Sharp have been recorded in upland streams of the northern jarrah forest (Aquatic Research Laboratory 1988; Bunn *et al.* 1986; Storey *et al.* 1990).

The provisionally identified *Glacidorbis* sp., from South Yeagarup Lake, is of interest because the only previous representative from Western Australia, *Glacidorbis occidentalis* Bunn & Stoddart, is highly associated with intermittently flowing streams (Bunn *et al.* 1989). The genus is known from both lotic and lentic waters in eastern Australia (Ponder 1986).

The species richness of the fauna was high, in both a regional and State context, to the extent that many of the lakes could be considered environments with high conservation significance. Species richness of invertebrates provides a useful comparison for different aquatic systems, with more diverse systems being considered 'healthier' than less diverse ones (Magurran 1988). Table 7 shows a comparison of species richness for invertebrates from different biogeographic regions of Western Australia. Species richness was high for lakes from both the Swan Coastal Plain and the south coast regions. The permanent lakes of the Swan Coastal Plain were characterised by nutrient enrichment to an extent where many were eutrophic, and the lakes were sampled on more than one occasion (Davis *et al.* 1993), which would have substantially increased the total species list. Sampling in summer/autumn would be likely to increase the total number of species for the south coast lakes. The major differences in species composition were that only about 30% of the identified species were shared by lakes in the two regions, with high numbers of species of Coleoptera in the Swan Coastal Plain lakes and high numbers of species of Chironomidae in the south coast lakes.

Multivariate classification of the lakes on the basis of invertebrate community structure and subsequent correlation with environmental parameters illustrated a tight coupling. Multiple discriminant analyses using TWINSPAN groupings produced an approximately 98% correct classification, suggesting that a model can be derived where by the type of invertebrate community can be predicted with a very high degree of accuracy, given a set of environmental parameters collected during winter/spring. Any departure from this predictive success could indicate some level of disturbance.

The most important environmental parameters, determined by multiple discriminant analyses to be significantly associated with invertebrate community structure, were

Table 7

Species richness of invertebrates recorded from a range of methodologically similar studies of lentic systems in Western Australia.

System	Catchment	Lakes	Seasonal sampling	Species richness	Reference
South coast lakes	mostly undisturbed	23	limited	209	this paper
Two Peoples Bay Lakes (south coast)	mostly undisturbed	3	yes	123	Storey et al. 1993
Robe River pools (Pilbara)	mostly undisturbed	10	limited	80	Streamtec 1991a
Swan Coastal Plain lakes	urban	5	yes	87	Davis & Rolls 1987
Swan Coastal Plain lakes	urban	6	yes	176	Balla & Davis 1993
Swan Coastal Plain lakes	urban	41	yes	253	Davis et al. 1993
Tamworth Lake (Swan Coastal Plain)	rural	1	no	48	Streamtec 1992
Collie wetlands	semi-disturbed rural	2	no	31	Streamtec 1991b
Swamphen Lake (Capel)	disturbed, revegetated	1	no	44	Cale & Edward 1990

levels of salinity, pH and nutrient status. All the lakes had salinities well below 3 g l⁻¹ considered the upper limit for biological freshwater (Bayly & Williams 1973). However, the higher salinities, with a maximum of 1626 mg l⁻¹ at Lake Davies in winter, appeared sufficient to cause a localised loss of some, presumably less-tolerant, species. Differences in the geologies and origins of the lakes, particularly recent past connections to the sea, however, also need to be considered.

Two of the indicator species determined by the TWINSPAN analysis were associated with dark coloured, acidic water. *Aphroteniella filicornis*, which is usually found in the lower order streams throughout Australia, has been recorded in perched acid, dune lakes on Fraser Island, Queensland (Cranston & Edward 1992). In this study, it only occurred in the acid dark-water lakes. The most commonly collected species of Ostracoda was *Gomphodella* aff. *maia* De Dekker which was mainly associated with the black-water acidic lakes.

The Trichoptera *Oecetis* sp., was an important indicator species for the separation of lakes Quininup, Davies, Owingup, Boat Harbour 3, Saide and Powell from the other lakes in the TWINSPAN analysis. This genus is common in eutrophic lakes of the Swan Coastal Plain (Balla & Davis 1993) and in lower rivers of the northern jarrah forest (Storey *et al.* 1990). Lakes Powell, Saide, Owingup and Boat Harbour 3 had both elevated salinity and nutrients and contained fauna more typical of the eutrophic lakes of the Swan Coastal Plain including the species *Daphnia carinata, Triplectides australis* Navas, *Sarscypridopsis aculeata* (Costa), *Austrochiltonia subtenuis* (Sayce), *Palaemonetes australis* Dakin, *Chironomus occidentalis* Skuse and *Polypedilum nubifer* (Skuse) (Balla & Davis 1993; Pinder *et al.* 1991). *Candonocypris novaezelandiae* (Baird) is often associated with eutrophic water (De Deckker

1981) and was only recorded from lakes 12046 and Powell. The high zooplankton biomass in Lakes 12046 and Powell consisted mainly of *Daphnia carinata* and this species was also the dominant species of Cladocera in the eutrophic lakes on the Swan Coastal Plain (Davis & Rolls 1987; Davis *et al.* 1993). Multivariate analyses showed that the structure of the invertebrate fauna of lakes Powell and Saide was highly associated with nutrient enrichment. Past and present land practices within the catchments of these lakes may have degraded water quality and subsequently adversely affected composition of the invertebrate fauna. The absence of *Calamoecia* from lakes Saide and Powell may reflect human activity in these eutrophic lakes. However, the geological history of the lakes should also be considered, as the only record of the euryhaline estuarine species *Gladioferens imparipes* Thompson was from Lake Powell, indicating a recent past connection with the sea. Lake Saide is associated with farming activities, particularly, in the past, with potato production. Lake Powell receives large nutrient inputs *via* Five and Seven Mile creeks, of secondary treated sewage from the Timewell Road Treatment Plant, Albany (Water Authority of Western Australia 1989b). Human activity should therefore be considered as a possible cause of elevated nutrient status for all of the eutrophic lakes.

Growns *et al.* (1993), using multivariate analysis of invertebrate data from 33 wetlands on the Swan Coastal Plain, found that the majority of wetlands could be grouped on the basis of nutrient status and colour, and concluded that low nutrient levels and highly coloured waters were the probable state of wetlands prior to European settlement. If this conclusion is correct, then many of the dark-water lakes of the south coast would have a high conservation status.

Analysis of the total species dataset by DECORANA (Fig 4) showed a gradient of putative conservation status of the

lakes, from 'high' quality, having low scores on axis one (*e.g.* lakes Doggerup, Smith, Wilson, Quitjup, Williams and Maringup), through 'intermediate' quality lakes (those in the centre of the axis and including Boat Harbour Lake 3, Lake Davies, Owingup Swamp and Lake 12046) to 'low' quality, having high axis one scores (*e.g.* lakes Powell and Saide). This nominal conservation status of the lakes, based on invertebrate community structure, was reiterated on the important underlying gradients. pH, salinity and phosphorus concentration respectively are the most important environmental parameters describing the above pattern. Future management programmes should include the routine monitoring of these parameters.

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Appendix 1. Species richness and list of taxa identified from the benthic, sweep and zooplankton samples and zooplankton biomass (dry weight) in a standard 50 m trawl. W = winter, S = spring. * = open water inaccessable. Numbers represent abundance categories for each species in any of the samples; 1 = < 50, 2 = 50–500, 3 = > 500 individuals. An 'A' after the taxa = adult—Coleoptera only. Lake numbers as in Figure 1.

	1S	2W	2S	3W	4W	5W	6W	6S	7S	8W	8S	9S	10S	11W	11S	12S	13S	14W	15W	15S	16S	17W	18W	19W	20W	21W	22W	23W	23S
Species richness (total taxa)	28	18	18	35	22	28	43	38	55	33	25	45	56	51	50	33	43	28	38	41	45	32	34	39	29	37	25	31	33
Zooplankton biomass (mg)	30.6	81.9	47.8	143.9	57.6	86.6	18	72.8	20.2	83.1	11.9	31.3	*	0	24.2	67.5	18.8	7.4	117	34.5	24.3	43.4	39.4	35.1	764.3	68.9	16.5	679	587
CNIDARIA																													
Hydra sp.	2											1	1													1			
PLATYHELMINTHES																													
TEMNOCEPHALOIDEA																													
Temnocephala sp.					1																		1						
TURBELLARIA																													
Dugesiidae sp. 1																												1	
NEMATODA																													
Nematoda spp.	2	1	1	1	3	2	1	1	1	1	1	1	2	2	2	1	1	1	2	1	1	1	1	1	1	3	1	2	1
MOLLUSCA																													
BIVALVIA																													
Bivalva sp. 1																					1								
Bivalva sp. 2																												1	
Westralunio carteri Iredale											1								1				1						
GASTROPODA																													
?*Glacidorbis* sp.														1															
Ferrissia petterdi (Johnston)	1			1										1							1	2	1	1					
Gastropoda sp. 1	3																												
Gastropoda sp. 2																			1	1									
?*Physastra*														1				1	1		1		1				1	1	2
ANNELIDA																													
OLIGOCHAETA																													
Oligochaeta spp.	3	2	1	1	3	1	1	1	2	2	1	1	1	1	1	1	2	1	2	1	2	1	2	2	2	1	1	2	1
HIRUDINEA																													
Richardsonianidae sp. 1																			1	1	2	1							1
Glossiphoniidae sp 2				1																									
ARTHROPODA																													
ARACHNIDA																													
Hydracarina sp. C								1																					
Hydracarina sp. D									1																				
Hydracarina sp. E							1									1	1												
Hydracarina sp. F						1	1	1	1					1		1	1	1		1					1	1			
Hydracarina sp. G	1				1				1					1		1	1	1		1		1	1		1	1			
Hydracarina sp. I					1				1					1			1		1						1				
Hydracarina sp. J									1			1						1											1
Hydracarina sp. L															1														
Hydracarina sp. O															1														
Hydracarina sp. Q															1		1												
Hydracarina sp. R					1	1	1	1				1	1	1		1	1	1	1	1					1	1			
Hydracarina sp. S							1	1																	1	1			
Hydracarina sp. T			1		1		1	1	1	1									1										
Hydracarina sp. U												1																	
Hydracarina sp. V																		1											
CRUSTACEA																													
Cladocera																													
Biapertura nr. *setigera* Brehm	1							1				1	1			1	1				1			1					
Bosmina meridionalis Sars			3												1				3										
Chydorus sp. Leach	1		2				1	1	1			1	1	1	1	1					1			1					
Neothrix cf. *armata* Gurney							1	1				2	1			1													
Daphnia carinata King																					1				3			3	3
Alonella sp.			1	1			1	1						1		1	1	1			1				1				
Cladocera undescribed genus V13									1							1	1								1				
Cladocera ?genus V16									1																				
Cladocera ?genus V17									1																				
Cladocera ?genus V18																							1						
Cladocera ?genus V15																													2
Graptoleberis testudinaria Sars												2					1	1											
Camptocercus cf. *australis* Sars														1			1								1				
Ostracoda																													
Newnhamia fenestra King									1			2																	
Cypretta baylyi McKenzie									1			2		1															
Newnhamia sp. 295														1															
Sarscypridopsis aculeata (Costa)	3													1										1	1	1		2	2
Limnocythere mowbrayensis Chapman		1															1												
Candonopsis tenuis (Brady)			1		1				1	1				1	1				2	1	1	1		1					
Gomphodella aff. *maia* De Deckker			1		1		1	1	2	1					2	1		2	1				3	1			1		
Cyprididae undescribed genus											1	2									1	1	1				1		
Alboa worooa De Deckker												1								2	1	1	2						
Ilyodromus sp. 255														1		1	1	1									1		
Paralimnocythere sp. 262																		1									1		
Candonocypris novaezelandiae (Baird)																										1		2	1

	1S	2W	2S	3W	4W	5W	6W	6S	7S	8W	8S	9S	10S	11W	11S	12S	13S	14W	15W	15S	16S	17W	18W	19W	20W	21S	22W	23W	23S
Species richness (total taxa)	28	18	18	35	22	28	43	38	55	33	25	45	56	51	50	33	43	28	38	41	45	32	34	39	29	37	25	31	33
Zooplankton biomass (mg)	30.6	81.9	47.8	143.9	57.6	86.6	18	72.8	20.2	83.1	11.9	31.3	*	0	24.2	67.5	18.8	7.4	117	34.5	24.3	43.4	39.4	35.1	764.3	68.9	16.5	679	587
Copepoda																													
Cyclopoida																													
Cyclopoida spp.	1	1	1	1	1	1	1	1	1	1		1	2	1	1	1	1	1	1	1	1	1	2	1	1	1	1	2	1
Harpactacoida																													
Harpactacoida spp.		1	1		1		1	1				1	2	1	1		1	1		1	1		2	1		1		3	1
Calanoida																													
Calanoida sp.																											2		
Calamoecia tasmanica (Smith) s.l.	3	3	2	3		3	3	3		3	3	2	1	1	3	3	3	1	3	3	3	3	3	2	3	3			
Calamoecia attenuata Fairbridge				3	1	1		3	1	3	2	1	1				3			3				1	1	3			
Hemiboeckella searli Sars							2																						
Hemiboeckella andersonae Bayly											1		1	1										1	1				
Gladioferens imparipes Thompson																													1
Isopoda																													
Phreatoicidea																													
Phreatoicidea sp. A																	1								1				
Amphipoda																													
Amphipoda sp. A														1			1												
Amphipoda sp. B																							1						
Gammaridae																													
Perthia branchialis (Nicholls)																									2				
Perthia acutitelson Straskraba	1			1		1	1		1			1	1	1	1	1	1		2	1	1				1		2		
Ceinidae																													
Austrochiltonia subtenuis (Sayce)	3	3	2	1			1	1	2	2		1							2	1	2	1	2			3	2	3	1
Decapoda																													
Parastacidae																													
Cherax sp. (immature)														1									1						
Cherax quinquecarinatus (Gray)				1	1		1	1	1						1	1	1	1	1	1				1					
Cherax tenuimanus (Smith)		1				1			1			1																	
Cherax destructor Clark																				1					1				
Palaemonidae																													
Palaemonetes australis Dakin		3	3	3	2				1			2					1		3	2	2	2	1				2	3	3
INSECTA																													
Ephemeroptera																													
Leptophlebiidae																													
Leptophlebiidae sp.						1																							
Neboissophlebia occidentalis Dean							1		1																				
Bibulmena kadjina Dean							1		1							1													
Baetidae																													
Cloeon sp.	1										1																		
Caenidae																													
Tasmanocoenis tillyardi (Lestage)			1				1	1		1	1	1	1	1	1				1	1					1	2	1	1	
Odonata																													
Odonata sp.							1							1															
Aeshnidae																													
Aeslina brevistyla (Rambur)								1				1	1															1	
Libellulidae																													
Orthetrum caledonicum (Brauer)																					1				1				
Austrothemis nigrescens (Martin)												1											1						
Corduliidae																													
Lathrocordulia metallica (Tillyard)												1																	
Hesperocordulia berthoudi (Tillyard)						1																							
Hemicordulia australie (Rambur)								1																					
Procordulia affinis (Selys)												1		1							1	1							
Synthemidae																													
Synthemis cyanitincta (Tillyard)														1															
Gomphidae																													
Austrogomphus lateralis (Selys)			1																										
Hemigomphus armiger (Tillyard)																	1												
Austrogomphus collaris Hagen												1									1								
Lestidae																													
Austrolestes annulosus (Selys)	1											1																	
Megapodagriidae																													
Austroagrion cyane (Selys)												1															1		
Coenagriidae																													
Coenagriidae sp.																											1		
Hemiptera																													
Corixidae																													
Micronecta sp.														1											1	1	1		2
Agraptocorixa sp. A		1																								1	1		
Sigara sp.																										1			1
Agraptocorixa sp. B																											1		
Veliidae																													
Veliidae sp. 2											1																		
Notonectidae																													
Notonectidae sp.											1																		
Anisops sp.	2										1														1			1	2
Notonecta sp.											1																		

	1S	2W	2S	3W	4W	5W	6W	6S	7S	8W	8S	9S	10S	11W	11S	12S	13S	14W	15W	15S	16S	17W	18W	19W	20W	21S	22W	23W	23S
Species richness (total taxa)	28	18	18	35	22	28	43	38	55	33	25	45	56	51	50	33	43	28	38	41	45	32	34	39	29	37	25	31	33
Zooplankton biomass (mg)	30.6	81.9	47.8	143.9	57.6	86.6	18	72.8	20.2	83.1	11.9	31.3	*	0	24.2	67.5	18.8	7.4	117	34.5	24.3	43.4	39.4	35.1	764.3	68.9	16.5	679	587

Nepidae
Ranatra sp.

Diptera
Chironomidae

	1S	2W	2S	3W	4W	5W	6W	6S	7S	8W	8S	9S	10S	11W	11S	12S	13S	14W	15W	15S	16S	17W	18W	19W	20W	21S	22W	23W	23S
Ranatra sp.												1																	
Paramerina levidensis (Skuse)						1	1	2	1	1		1		1	1	1	1	1	1	1		1	1	1		1		1	1
Procladius paludicola Skuse						1			1											1	1				1				
Procladius villosimanus Kieffer														1		1												1	1
?Zavrelimyia sp. V20						1			1					1		1		1					1						
Macropelopia dalyupensis Freeman		1	1											1			1							1					
Macropelopia sp. VSCL50																1													
Ablabesmyia sp. V37												1		1		1													
Coelopynia pruinosa Freeman				1										1														1	1
Orthocladiinae sp. VSCL3	1																												
Orthocladiinae sp. VSCL7		1																											
Orthocladiinae sp. VSCL20				1					1										1	1									
Orthocladiinae sp. VSCL36								1																1	1		1		
Orthocladiinae sp. VSCL38								1				1								1	1								
Orthocladiinae sp. VSCL43													1	1	1														
Orthocladiinae sp. V43												1								1					1				
Cricotopus annuliventris (Skuse)												1	1																
Corynoneura sp.	1																												
Limnophyes pullulus (Skuse)	1			1				1	1			1	1	1		2	1	1	1		1	1	1			1			1
?Limnophyes sp. V31				1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1						
?Limnophyes sp. VSCL45																								1					
Thienemanniella sp. V19									1					1		2	2	2											1
Stictocladius sp. VSCL24							1										1												
Dicrotendipes sp. V47	1						1	1		1	1		2		1	1	1	1	1	1	1	1	1	1	1		1		1
Dicrotendipes ?conjunctus Walker			1																						1				
Kiefferulus martini Freeman																									1			1	1
Kiefferulus intertinctus Skuse			1	1	1				1			1	1	1	1	1				1					1			1	1
Cryptochironomus griseidorsum Kieffer				1			1	1									1												
Nilothauma sp.					1																				1				
?Stenochironomus sp.				1							1																		
Stenochironomus sp. VSCL14				1					1		1																		
Stenochironomus sp. VSCL31				1					1	1	2			1	1	1	1									1			
Riethia sp. V5									1	1				2	1	1	1									1			
Riethia sp. V4		1	1	1	1	1			1	1	1	1	1	1	1			1	1	1	1	1							
Polypedilum sp. VSCL8				2						1				1	1									1			1		
Polypedilum sp. VSCL16									1		1		1	1	1	1	1							1					
Polypedilum sp. VSCL33																								1				1	
Polypedilum nubifer (Skuse)																												1	
Chironomus occidentalis Skuse								1	1			2				1			1				1						
Chironomus aff. *alternans* Walker									1				1			1				1	2	1	1						
Cladopelma curtivalva Kieffer						1		1		1	1			1	1		1								1				
Harnischia sp. VCD10							1																						
Chironomini ?genus VSCL27								1	1	1	1	1	1	1		1													
Chironomini ?genus VSCL34												1	1											1					
Chironomini ?genus VSCL35								1	1											1									
Tanytarsini ?genus	2		1	1		1	1	1	1			1	1	1	1	1	1	1	1	1	2	1	1	1				1	1
Tanytarsus sp VSCL5		1	1		1														1	1	1								
Tanytarsus sp. VSCL9			2		1	1		1	1							1													
Tanytarsus sp. VSCL18	1	1	1	1	1			1	1	1								1	1	2	2	1	1	1	1		1		
Cladotanytarsus sp. VSCL10			1					1	1	1		1		1												1			
Stempellina ?australiensis Freeman			2		1	1	1	1	1	1	1														1				
Aphroteniella filicornis Brundin														1	1		1					1	1		1	1	1	1	

Ceratopogonidae

	1S	2W	2S	3W	4W	5W	6W	6S	7S	8W	8S	9S	10S	11W	11S	12S	13S	14W	15W	15S	16S	17W	18W	19W	20W	21S	22W	23W	23S
Ceratopogonidae sp. B						1	1							1	1		1					1	1		1	1	1	1	
Ceratopogonidae sp. F						1																							
Ceratopogonidae sp. G					1			1																				2	2
Ceratopogonidae sp. K									1											1				1					
Ceratopogonidae sp. L				1			1																	1					
Ceratopogonidae sp. N						1											1			1	1			1					
Ceratopogonidae sp. O																						1		1					
Ceratopogonidae sp. P						1																1		1					

Tipulidae

	1S	2W	2S	3W	4W	5W	6W	6S	7S	8W	8S	9S	10S	11W	11S	12S	13S	14W	15W	15S	16S	17W	18W	19W	20W	21S	22W	23W	23S
Limoniinae sp. A																		1					1		1		1		
Limoniinae sp. B	1												1																
Limoniinae sp. F															1														

Empididae

	1S	2W	2S	3W	4W	5W	6W	6S	7S	8W	8S	9S	10S	11W	11S	12S	13S	14W	15W	15S	16S	17W	18W	19W	20W	21S	22W	23W	23S
Empididae sp. A					1									1															
Empididae sp. B														1															

Tabanidae

	1S	2W	2S	3W	4W	5W	6W	6S	7S	8W	8S	9S	10S	11W	11S	12S	13S	14W	15W	15S	16S	17W	18W	19W	20W	21S	22W	23W	23S
Tabanidae sp. A			1																		1		1						

Dolichopodidae

	1S	2W	2S	3W	4W	5W	6W	6S	7S	8W	8S	9S	10S	11W	11S	12S	13S	14W	15W	15S	16S	17W	18W	19W	20W	21S	22W	23W	23S
Dolichopodidae sp. A																											1		

Culicidae

	1S	2W	2S	3W	4W	5W	6W	6S	7S	8W	8S	9S	10S	11W	11S	12S	13S	14W	15W	15S	16S	17W	18W	19W	20W	21S	22W	23W	23S
Culicidae sp.	1																												

	1S	2W	2S	3W	4W	5W	6W	6S	7S	8W	8S	9S	10S	11W	11S	12S	13S	14W	15W	15S	16S	17W	18W	19W	20W	21S	22W	23W	23S
Species richness (total taxa)	28	18	18	35	22	28	43	38	55	33	25	45	56	51	50	33	43	28	38	41	45	32	34	39	29	37	25	31	33
Zooplankton biomass (mg)	30.6	81.9	47.8	143.9	57.6	86.6	18	72.8	20.2	83.1	11.9	31.3	*	0	24.2	67.5	18.8	7.4	117	34.5	24.3	43.4	39.4	35.1	764.3	68.9	16.5	679	587
Ephydridae																													
Ephydridae sp. A																						1							
Trichoptera																													
Ecnomidae																													
Ecnomidae sp.						1																							
Ecnomina ?trulla Neboiss							1	1	1						1		1												
?Ecnomus sp.				1		1	1								1	1													
Ecnomus pansus Neboiss						1											1												
Ecnomus turgidus Neboiss																								1					1
Leptoceridae																													
Leptoceridae spp.		1					1			1					1		1	1			1	1			1				
Lectrides parilis Neboiss																				1					1				
Triplectides sp. B																										1			
Notoperata tenax Neboiss												1			1														
Notalina sp. A																									1				
Oecetis sp.		1																			1		1		1		1		
Triplectides australis Navas																												1	1
Leptoceridae sp. C			1						1			1					1												
Leptoceridae sp. F						1	1	1	1						1	1	1							1	1				
Leptoceridae sp. H								1										1						1					
Leptoceridae sp. I												1			1	1													
Hydroptilidae																													
Hydroptilidae sp.									1			1			1		1												
Acritoptila globosa Wells						1	1	1							1	1													
Hellyethira sp. B					1							1									1	1		1					
Atriplectididae																													
Atriplectides ?dubius Mosley															1														
Polycentropodidae																													
Polycentropodidae sp.								1													1								
Plectrocnemia eximia Neboiss															1														
Coleoptera																													
Dytiscidae																													
Sternopriscus ?browni Sharp															1	1		1											
Sternopriscus sp. A															1														
Liodessus sp.															1														
Megaporus sp.											1																		
Homeodytes scutellaris (Germar)			1								1																		
Homeodytes sp.							1																						
Sternopriscus browni Sharp A	1	2		1	1	1	1	1			1	1			1						1						1	1	
Sternopriscus marginata Watts A			1	1		1									1									1					
Rhantus sp. A																							1						
Liodessus inornatus (Sharp) A																					1		1	1					
Necterosoma darwini (Babington) A																							1						
Antiporus femuralis (Boheman) A								1								1										1			1
Megaporus howitti (Clark) A																													1
Megaporus solidus (Sharp) A	1	2																					1			1			
Homeodytes scutellaris (Germar) A																				1									
Lancetes lanceolatus Clark A											1									1			1						1
Liodessus dispar (Germar) A	1							1															1			1			
Megaporus sp. A									1																				
Helodidae																													
Helodidae								1		1	1						1		1			1	1		1		1		
Gyrinidae																													
Macrogyrus sp. A																		1	1										
Hydrophilidae																													
Hydrophilidae sp. 6																													
Hydrophilidae sp. 1 A	2							1															1						
Hydrophilidae sp. 2 A								1													1								
Hydrophilidae sp. 3 A																					1								
Hydrophilidae sp. 9 A																									1				1
Hydrophilidae sp. 11 A																											1		1
Carabidae																													
?Carabidae sp. A																									1				
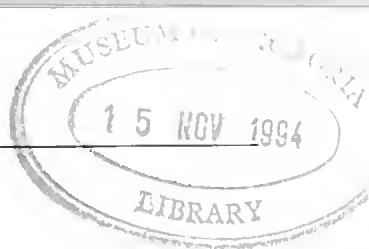
Biosystematics of Australian mygalomorph spiders: Description of a new species of *Aname* and its aerial tube (Araneae: Nemesiidae)

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Abstract

A new species of the Australian mygalomorph genus *Aname* is described. The species has an unusual burrow structure which consists of a soil-plastered tube that extends into the foliage of a supporting shrub. It is postulated that the aerial tube is an anti-flooding adaptation and that the spider has secondarily become a forager amongst foliage. Such a tube and behaviour have not been recorded for any other Australian mygalomorph spider.

Introduction

This paper is the first in a planned series in which new species of *Aname* will be described and their respective biology discussed. The endemic nemesiid genus *Aname* Koch is the most widely distributed of all Australian mygalomorph genera. It occurs all over the continent in diverse habitats (Main 1972; Raven 1981, 1984a, b, 1985), in Tasmania (Hogg 1902; Raven 1984b) and on several offshore islands (Main 1976, 1982). Main (1985) recognised 14 nominal species and indicated that there are many undescribed species. Raven (1981) synonymised *Chenistonia* with *Aname*, a decision not concurred with by Main (1985). Raven later (1984a, b, 1985) attributed 17 new species from northern and eastern Australia and one from Tasmania to *Aname*. Of these, Main (1985) listed two in *Chenistonia*.

Main (1993) gave a summary account of anti-flooding burrow specialisations of some mygalomorph species. Included amongst the specialisations, were listed those of nests of some species which characteristically construct nests on the trunks of trees, and which have no contact with the ground, *e.g.* of certain theraphosids, *Sason* (Barychelidae), *Conothele* (Ctenizidae), *Chenistonia villosa* Raibow and Pulleine (Nemesiidae) and *Moggridgea tingle* Main (Migidae). In addition, it is well known that some species of the notorious Australian funnel web spiders, *Hadronyche* (of which some species have been cited as *Atrax* species) similarly construct silk tubes on the bark and trunks of trees (Gray 1978, 1981, 1984, 1988 ; McKeown 1962; Mascord 1970; Main 1964, 1976), sometimes as high as 15m above ground (Gray 1981).

Main (1993) also described the aerial tube of an unnamed *Aname* species. The nest of this species is unique in that, while other arboreal mygalomorphs have their tubes associated with the trunk or branches of trees, the *Aname* species has its tube extending into foliage. Main postulated that this aerial tube, which is supported by spinifex *(Triodia)* tussocks or chenopod shrubs, primarily prevents flooding of the burrow during sudden deluges, and that secondarily it

has exposed the spider to a new foraging situation (for a mygalomorph) *i.e.* within the foliage of plants.

While descriptions of numerous new species of *Aname* are in progress, this species has been singled out here for description because of its noteworthy burrow structure and distinctive foraging behaviour.

Systematics

Abbreviations

BYM, Barbara York Main collection (housed in the Zoology Department, University of Western Australia). **SAM**, South Australian Museum. **WAM**, Western Australian Museum. **SA**, South Australia. **WA**, Western Australia.

ALE, anterior lateral eyes; **AME**, anterior median eyes; **PLE**, posterior lateral eyes; **PME**, posterior median eyes. **v**, ventral; **d**, dorsal; **p**, prolateral; **r**, retrolateral (in reference to position of leg spines).

Aname turrigera sp. nov.
(Figures 1 A - M, 2 A - B, 3 ; Table 1)

Holotype: Female , 24 km W of Balladonia Roadhouse, Eyre Highway, W A (32°15′ S 123°2′ E), collected by B Y Main, 20 November 1986 (BYM 1986/174, WAM 92/2629).

Paratype: Female (internal genitalia figured), data as for holotype (BYM 1986/173, WAM 92/2630).

Other paratypes: (all collected by B Y Main unless otherwise stated).

Western Australia: 3 females, same data as holotype (BYM 1986/175, 176, 177); 2 females, same locality as holotype, 24 May 1986 (BYM 1986/157, 158); female with brood, data as for preceding (BYM 1986/159); female, Mallura, A R Main, 21 August 1960 (BYM 1960/19).

South Australia: 2 females, 18 km west of Lock, 8 May 1986 (BYM 1986/29, with brood young; BYM 1986/60 (SAM N1994396) internal genitalia dissected); 3 females and one
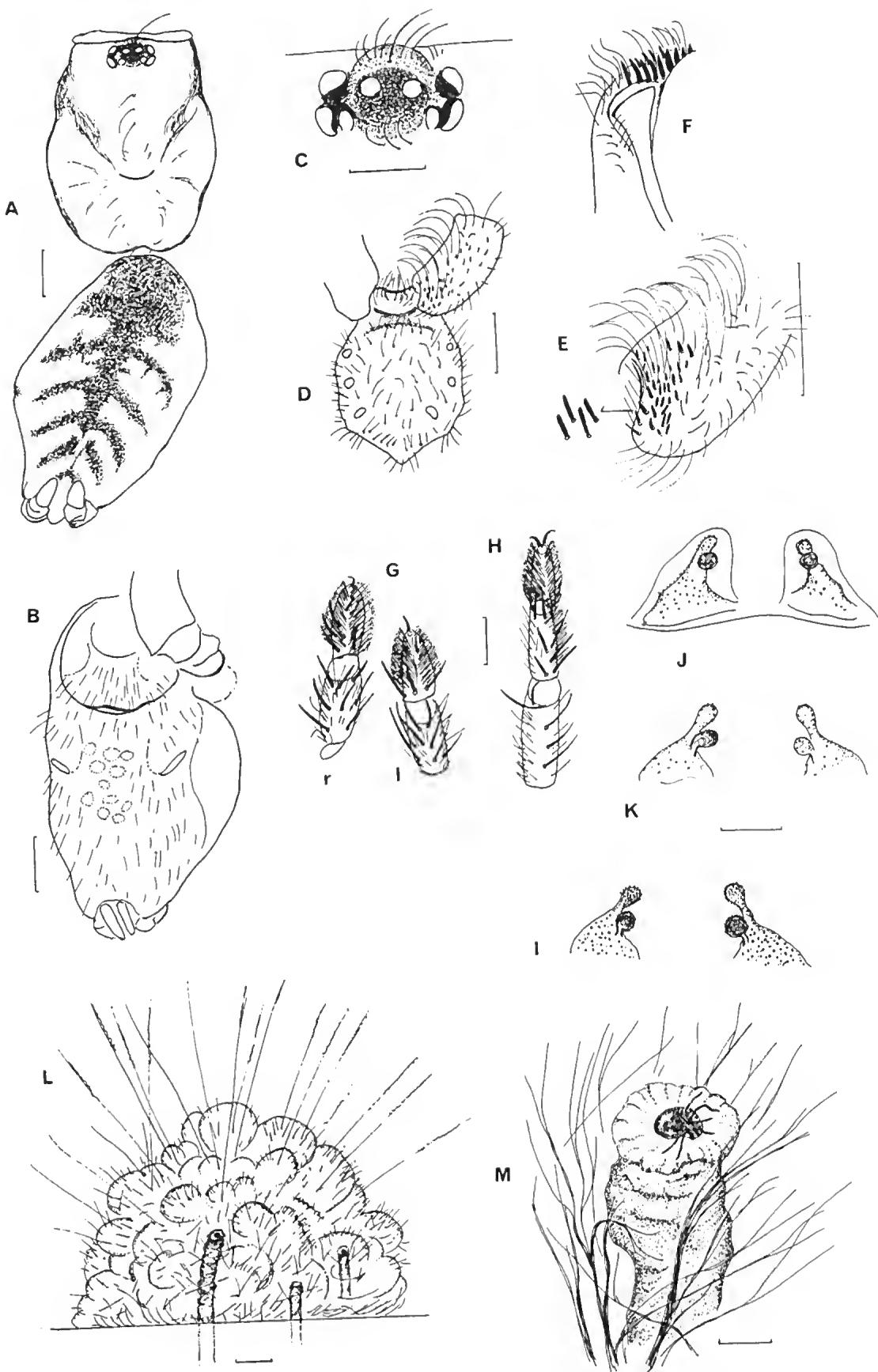
Figure 1. *Aname turrigera* , female (holotype). **A**, Dorsal view of spider, carapace and abdomen. **B**, Abdomen, ventral. **C**, Eyes. **D**, Sternal area. **E**, Maxillary cuspules. **F**, Pseudorastellum. **G**, Palp tarsi and metatarsi, r = right, l = left. **H**, Left leg I, ventral, tarsus, metatarsus, tibia. **I, J, K**, Female internal genitalia; **I**, (BYM 1986/173) W Balladonia, **J**, (BYM 1986/110) Yalata, **K**, (BYM 1986/60) W of Lock. **L**, Spinifex tussock with aerial tubes. **M**, Spider in foraging position at entrance of tube (adapted from photograph by D Hirst). Scale bars: **A, B, D, E, G, H** = 1.0 mm; **C** = 0.5 mm; **F**, not to scale; **I - K** = 0.5 mm; **L**, = 10.0 cm; **M** = 1.0cm.

cast skin (separate burrow) same locality as preceding, 18 May 1986 (BYM 1986/98, 99, 101, 102); female, 29.6 km north of Minnipa, 16 May 1981 (BYM 1981/4); 2 females, Yalata (Yalata Swamp, Head of the Bight), 20 May 1986 (BYM 1986/109; 110 internal genitalia dissected); female, Ardrossan, 16 May 1986 (BYM 1986/67) (tentative identity).

Description is of holotype except where otherwise stated. Male unknown.

Female . *Colour* generally tan brown, abdomen dorsally with dark bands on pale yellowish background, venter pale. *Carapace* glabrous, with light covering of fine hairs; length 4.6 mm, width 3.5, caput width 2.4. *Eye tubercle* 0.4 long, 1.0 wide, pronounced anterior mound. Eye diameters: ALE 0.25, AME 0.15, PLE 0.2, PME 0.1; AME apart 0.2, ALE apart 0.65. *Fovea* procurved. *Chelicerae* with long heavy apical teeth (pseudorastellum). Teeth on groove of paturon irregular sizes, prolateral 10 (right), 7 (left), without basal retrolateral teeth. *Sternum* length 2.5, width 2.2; sigilla, posterior pair ovoid, submarginal. *Labium* length 0.4, indented anteriorly. *Maxillae* with about 35 long, thin pin-like cuspules. *Legs*. *Scopula* complete on tarsi of palp, legs I and II (without dividing line of bristles), and metatarsi I; on metatarsi II complete on retrolateral aspect and apical half only of prolateral aspect; absent on legs III and IV which have dense bristles on tarsi. Paired *tarsal claws* I and II with uniform comb of at least six or seven teeth respectively on each claw; III with fewer teeth , inner rows with fewer teeth and distal to outer rows; IV, teeth present only on "outer" edges of claws, prolateral claw with 3 prolateral teeth, retrolateral claw with 3 or 4 basal retrolateral teeth. *Spines* absent on all leg tarsi. Palp tarsus v 5 (right), v 4 (left - arranged as 1 apical and 3 in proximal line; this is the "typical" arrangement for most specimens - see under **Variation** and Fig 1 G). Leg I, metatarsus v 2-2-1-3 (apical), tibia v 5. II, metatarsus v 2-1-3, tibia v (fine bristles) 1-1-1. III, metatarsus v 5, d 1-2, rd 4, tibia v (bristles) 1-1-2, d 2, p 2, r 2, patella p3 + dense thorn-like "spinules", r 2. IV, metatarsus v 9, r 3, tibia v (fine bristles) 1-1-2, r2. *Abdomen* with marked dorsal pattern of bars. *Spinnerets* with terminal segment of posterior lateral pair ovoid. *Internal genitalia* (Paratype WAM 92/2630, BYM 1986/173) bilobed, main lobe bottle shaped with broad "open" base, narrow neck and terminally bulbous; lateral lobe arising from main lobe below constriction of "neck" (Fig 1I).

Variation

Table 1

Leg dimensions of holotype female of *Aname turrigera*.

Leg formula = length of leg divided by carapace length. Tibial index = width of patella X 100 divided by length of tibia + patella (Petrunkevitch 1942).

Leg formula: 4/3.02, 1/2.2, 2/2.0, 3/1.73

	Femur	Pat	Tib	Mt	Ta	Total
I	3.2	2.0	2.0	1.8	1.3	10.3
II	2.7	1.8	1.8	1.7	1.2	9.2
III	2.2	1.4	1.2	1.9	1.3	8.0
IV	3.1	2.1	3.4	3.0	1.3	13.9
Palp	2.2	1.5	1.4	-	1.5	6.6

Width of patella I at knee = 0.6. Tibial index = 15.0.
Width of patella IV at knee = 0.7. Tibial index = 12.7.

Chelicerae , usually 6 or 7 prolateral teeth on groove of specimens with carapace length upwards of 3.5 mm (may be asymmetrical on individual specimens); 3 to 5 basal retrolateral teeth usually present (absent on holotype). Juvenile specimens (brood of BYM 86/159) with prolateral teeth. Labium of paratype (BYM 86/173) with a single long pointed cuspule. Some specimens (*e.g.* BYM 86/60, from Lock, Eyre Peninsula, S A) with short thorn-like spines on promargin of coxae I (absent on holotype). *Spines on palp tarsus* . While the typical number is like that of holotype , 1 distal and three in proximal row (left tarsus Fig 1 G), the number varies (unrelated to size or locality) as 1, 2, occasionally 3 distal spines, and 3 or rarely 4 proximal (17 sampled). *Carapace length/width* of females ranges from 3.5/2.8 (*i.e.* from smallest with apparent adult internal genitalia), 3.6/2.7 (female with brood young) to 4.7/3.5 (largest specimen collected). The internal genitalia of specimens from widely distant localities have a remarkably similar configuration (see Figs 1 I, J, K) *e.g.* Balladonia (paratype BYM 1986/173) carapace L/W 4.6/3.4); Yalata (BYM 1986/110) carapace L/W 4.2/2.3), Lock (BYM 1986/60, carapace L/W 3.5/2.8)

Etymology

The name *turrigera*, from the Latin (*turris-gero*) meaning "tower-bearing", in reference to the tower-like aerial tube.

Affinities

The species has some morphological features similar to *Kwonkan* Main and *Yilgarnia* Main, namely the configuration of the internal genitalia (see Main 1983 Figs 23 - 26, 1986 Fig. 1 h, i), a strong "pseudorastellum" and the pin-like maxillary cuspules characteristic of at least some *Kwonkan* species. It is assumed that the male will have a relatively short and broadly based embolus and a cluster of retrolateral short spines on the palp tibia like that of these two genera. Some undescribed species of *Aname* also share these male features. However no such specimens can be unequivocally attributed to *Aname turrigera* as none have been collected from the precise habitats of *turrigera* females. Nevertheless, the undescribed species and *Aname turrigera*, with further data may warrant erection of an inclusive new genus. On a cladistic analysis, *Kwonkan* and *Yilgarnia* would be placed as apomorphic derivatives from such a hypothetical genus.

Natural history

Geographic Distribution and Habitat

The distribution of *Aname turrigera* ranges from west of Balladonia to Eyre Peninsula, in patchily distributed favoured habitats. Although it has been collected from Mallura north of the Nullarbor Plain and in coastal, lagoon-like flats of the Yalata Swamp at the Head of the Bight (southeast of the Nullarbor), it has not been observed on the Plain proper or on coastal areas immediately to the south, such as the Roe Plain. The species *Aname turrigera* occurs in semi arid habitats but in situations which are subjected to periodic sheet flooding or inundation, such as *Melaleuca* summer-dry swamps (*e.g.* Eyre Peninsula), mallee/spinifex associations (*Eucalyptus / Triodia pungens*) sites which experience flooding especially during summer thunderstorms (*e.g.* west of Balladonia and Eyre Peninsula), flood-prone mulga (*Acacia aneura*) swales

in the sand dune country north of the Nullarbor Plain (*e.g.* Mallura) and saline flats dominated by chenopod shrubs (*e.g.* coastal "lagoons" of Yalata Swamp at the Head of the Bight).

Burrow structure and foraging behaviour

Main (1993) recorded the burrow and characteristic aerial tube extending from it of *Aname turrigera* . The vertical burrows are shallow (up to about 15cm deep) and lined with a thin, stocking-like silk tube which is loosely attached to the burrow wall. The tube extends from the burrow as a soil-encased turret into the supporting scaffold of a shrub (*e.g.* chenopod or glass wort) or spinifex (*Triodia*) grass tussock (Fig 1L, 2A). Turrets may be up to about 25 cm high and about 2 or 3 cm in diameter although the lumen is less than a centimetre. Occasionally shorter, and free standing, tubes have been observed (Fig 2B). The first turrets I observed were mistaken for termite flight towers. Turrets supported by foliage often have thick, irregularly "lumpy" walls, which suggests that the nests are deepened after rain when the soil is wet and gobs of spoil are dumped from the mouth of the tube from where some soil slides down the outside wall as a paste, while at the same time the turret is gradually heightened. As the soil dries out it would harden. Although burrows may be periodically flooded, the shrub-supported tubes (into which spiders can "escape") apparently persist and are heightened seasonally.

However, free standing tubes probably collapse during heavy rain, as they never attain the height of those supported in foliage.

As a consequence of the specialised burrow, which seems primarily associated with flood avoidance, the spiders have secondarily been exposed to a "new" foraging opportunity *i.e.* to catch prey amongst foliage (Main 1993). Presumably *Aname turrigera* catches prey from within reach of the tube entrance. David Hirst (*pers. comm.*) has observed and photographed a spider sitting with anterior legs splayed in typical "sit and wait" foraging pose in a turret entrance (see Fig 1M). It is also possible, as with some *Aname* species which forage at ground level, that *Aname turrigera* may sometimes "chase" prey (within the canopy) from an ambushing stance. Although a number of arboreal Australian mygalomorphs make tubes on tree trunks or against the boles of trees or stems of shrubs (see Main 1993), no other species have been observed to forage within a shrub canopy.

Life history

The reproductive phenology of *Aname turrigera* is not completely known. Two females with brood young have been collected. One from near Lock, S A on 8 May 1986 (BYM 1986/29) and the other on 24 May 1986, 24 km west of Balladonia Roadhouse (BYM 1986/159). The mean carapace length of 10 specimens from a sample of brood young collected from the burrow of the latter was 1.72 mm. It is not known when males wander, but by comparison with other species which release young from the burrow in autumn/winter, it is assumed that male wandering and hence mating would likewise be in association with autumn/winter rainy periods. Entrances of turrets are sometimes sealed with soil plugs during dry summer weather.

Figure 2. Aerial tubes of *Aname turrigera* . A, Tube in spinifex tussock, Lock, S A. **B**, Free standing tubes at base of mulga tree, Mallura, W A. Scale bars = 5.0 cm.
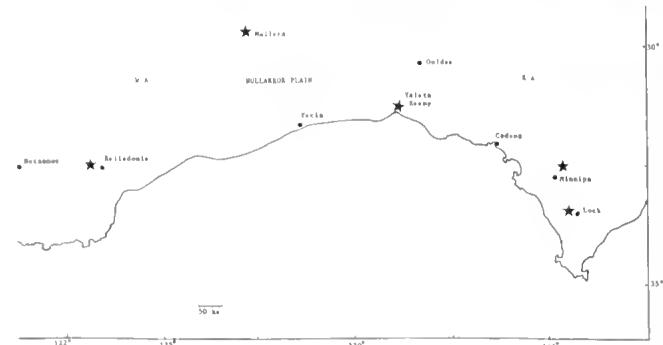

Figure 3. Map of south eastern Western Australia and Eyre Peninsula, South Australia, showing known distribution of *Aname turrigera* (excluding Ardrossan in Yorke Peninsula).

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Wet heathlands of the southern Swan Coastal Plain, Western Australia: A phytosociological study

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Abstract

Wet heathlands, formed by sclerophyllous nanophanerophytes and graminoids growing on seasonally waterlogged soil, were surveyed on the southern Swan Coastal Plain and classified using two-way indicator species analysis (TWINSPAN). Three main wet heathland groups were identified, these being the *Pericalymma - Hypocalymma, Pericalymma - Regelia* and *Melaleuca - Cassytha* alliances respectively. The *Pericalymma - Hypocalymma* alliance is found north of the Capel River in depressions in the Bassendean Dune system on colluvial sands which have impermeable organic, clay or ferruginous horizons at about a metre. The *Pericalymma - Regelia* alliance is found south of the Capel River primarily on colluvial wet sands, and shallow sands and loams, in the Abba soil association. Variations in vegetation composition within this alliance are associated with the depth to the impermeable layer (usually lateritic) and the winter height of the perched water table. The *Melaleuca - Cassytha* alliance was found north of the Capel River mainly on heavy clays formed from Quarternary alluvium within the Serpentine River Association. These heathlands were species poor compared to Australian dry heathlands, with the number of species per 100 m² ranging from 9 to 26. The ecology of these heathlands is discussed in the light of the limited information available. Their existence as fragmented islands within a primarily agricultural landscape makes them vulnerable to changes in ecosystem processes.

Introduction

Wet heathlands, which are plant formations dominated by evergreen sclerophyllous nanophanerophytes and graminoids growing on seasonally waterlogged soil (Groves & Specht 1965; Specht 1981), are widespread but of very limited area in the south west of Western Australia. Dry heathland, now generally termed kwongan, has been the subject of much scientific research in Western Australia over the last ten years (*e.g.* Brown & Hopkins 1983; Pate & Beard 1984; Bell & Loneragan 1985; Brown 1989), but wet heathland remains largely undescribed in regard to its phytosociology and ecology. Undoubtedly this is because wet heathland in Western Australia is much less extensive and less species rich than dry heathland.

Dry heathland or kwongan, most of which occurs on sandplain soils in the low to moderate (300-600 mm) rainfall areas of the South West Botanical Province, has been estimated to cover 118,000 km², or 27% of the province (Beard 1984). No comparable estimate of the area of wet heathland, which is virtually confined to the high rainfall (> 800 mm) areas of the south-west, is available. Because of its limited and scattered occurrence, wet heathland has usually been mapped in conjunction with sedgeland and "swamp vegetation" (Smith 1973; Beard 1981).

The dry heathland of the sandplains is extremely species rich at small (< 1 ha) sample sizes with an average of 60 species per 100 m² in the central wheatbelt (Brown 1989) and 70 per 100 m² in the lateritic uplands of the Mt Lesueur area (Hopkins & Griffin 1984). There are few published reports of species richness in Western Australian wet heathland. Wardell-Johnson *et al.* (1989) found an average of 21 species per 314 m² plot in a heathland community on damp shallow sandy sites near Walpole on the south-western coast. However, this study did not include herbaceous perennials and some annuals.

Much of the vegetation which originally included wet heathland communities has been cleared for agriculture and the area of this vegetation type left in Western Australia would probably cover no more than 500 km², with the most extensive areas being within the Warren Botanical Sub-district (Smith 1972). The wet heathland of the southern Swan Coastal Plain (SCP), which is the focus of this study, is primarily restricted to small conservation reserves and road verges surrounded by cleared farmland.

The main objective of this study was to characterize the wet heathland communities of the southern SCP in terms of their characteristic species and to relate these communities to soil and other environmental factors. Identification of the community types provides a framework to plan the management and conservation of these communities, which despite their relative paucity of species provide a habitat for many of the rare and endangered plant taxa of the high rainfall areas of the South West Botanical Province (Keighery & Robinson 1990).

Regional Setting

Geology, Geomorphology and Soils

All study sites were on the southern part of the Swan Coastal Plain (SCP), Western Australia, between latitude 33° 00' S and 33° 45' S (Fig 1). The SCP extends from the Darling and Whicher Scarps to the Indian Ocean and to about 60 m above sea level. The plain is underlain by the Phanerozoic sediments of the Perth Basin and several landform units lying parallel to the coastline and closely related to the geology can be identified (Wilde & Walker 1982). At the foot of the Darling Scarp is a zone comprised of coalesced colluvial fans and the remnants of a strandline deposit. This zone merges into a 10 km-wide alluvial plain (often called the Pinjarra Plain), which has been lateritized and then extensively stripped to form soils which are predominately meadow podzolic in nature (Mulcahy 1973). The meadow podzols consist of a sandy surface overlying a poorly structured clay of low permeability developed on a lateritic pallid zone. Along the streams which cross the plain, younger deposits in the form of terraces are incised into the meadow podzols and in places alluvial fans overly them. These younger soils are red and yellow podzolics and undifferentiated soils.

Figure 1. Wet heathland vegetation survey areas on the southern Swan Coastal Plain. 1. Riverdale Nature Reserve, 2. Reserve No. 20331, 3. Wellard Nature Reserve, 4. Guthrie Forest Block, 5. Byrd Swamp Nature Reserve, 6. Hay Park Recreation Reserve, 7. Reserve No. 1167, 8. Ruabon Nature Reserve, 9. Ruabon (railway reserve), 10. Williams Road (railway reserve), 11. Tutunup (railway reserve), 12. Yoongarillup Reserve, 13. Fish Road Reserve, 14. Ambergate Nature Reserve.

Further west, at least three generations of dune soils, overlying the fluviatile deposits, are evident. At the present coastline is the youngest dune system, the Quindalup System of McArthur & Bettenay (1960), which consists of highly calcareous shell sand deposited during the Holocene. Inland of this system lies a belt of slightly podzolized yellow sand overlying limestone called the Spearwood System (McArthur & Bettenay 1960). The Spearwood sands are almost entirely quartz although there are localized deposits of heavy mineral sands. Lying between the Spearwood System and the alluvial plain is the Bassendean System (McArthur & Bettenay 1960), composed of the oldest aeolian deposits, which have now lost their dune morphology. It is of lower relief than the younger dunes nearer the coast and the soils are highly leached and podzolized white quartz sands with B horizons of accumulated iron and organic matter. The depressions between these low dunes are filled with swamp and lacustrine deposits which may be peat, peaty sand, sand or clay (Wilde & Walker 1982).

Details of the soil associations of the three dune systems and the alluvial plain for the southern SCP are given by McArthur & Bettenay (1956, 1958), Pym & Poutsma (1957), McArthur (1958) and Tille & Lantzke (1990).

Climate

The climate of the area is "mediterranean" with cool wet winters and warm to hot, dry, summers (Gentilli 1972). Proximity to the coast provides a moderating influence and frosts are infrequent, with mean temperatures of the coldest and hottest months being 11-13°C and 25-29°C. Mean annual rainfall ranges from about 850 to 1000 mm through the study area with the higher levels occurring near the scarps. The pasture growing season is seven months, from April to October inclusive, and during this period the excess of rainfall over potential evapotranspiration of pastures is 560 mm at Harvey (Pym & Poutsma 1957) and 380 mm at Bunbury (McArthur & Bettenay 1956). This excess of water is available for run-off, storage in the sub-soil or penetration to the underlying aquifers. The flat topography of much of the coastal plain ensures that there is little run-off and where the subsoils are relatively impermeable much of this excess is probably stored in the subsoil and therefore is available for growth of deep rooted native species beyond the period of pasture growth (McArthur & Bettenay 1956).

Methods

Data collection

The fourteen reserve and roadside sites containing areas of wet heathland were visited, usually at least twice, in spring 1992 and 1993. At each site between three and eight 10 m x 10 m quadrats were sampled. Within each quadrat, all vascular plant species were either identified in the field or given a code number and collected for later identification. The nomenclature of Green (1985) and Marchant *et al.* (1987) was used. Each species was given a cover value between 1 and 5 on a modified Braun-Blanquet scale: 1, < 5%; 2, 5-25%; 3, 25-50%; 4, 50-75%; 5, 75-100%. At least one soil pit was dug at each site down to 1 metre, or to a limiting horizon. Soil texture of each horizon was recorded and samples were taken within each horizon for determination of the Munsell colour. Published soil surveys were also used to determine the soil type at each site and note was taken at the time of survey of the depth of watertable at each site.

Data analysis

Vegetation data were classified by two-way indicator species analysis using the polythetic divisive computer program TWINSPAN (Hill 1979) and the Braun-Blanquet cover value for each species. Only the 116 species which were found in at least two quadrats were used in the analysis. In general, classification was terminated at the third level of division to give three groups (alliances) and six subgroups (associations) of the 47 quadrats; a further sub-group was recognized at the fourth level of division. Groupings of less than four quadrats at the fourth level of division were not recognized. The taxonomic composition of the species groups was compared using the Sorenson coefficient of community (Gauch & Whittaker 1972). Detrended Correspondence Analysis (DCA; Hill & Gauch 1980) was used to ordinate the 47 quadrats so their relationship with identified edaphic variables could be examined.

Results

Vegetation and soils

The TWINSPAN classification produced three main groups of wet heathland species, which are termed **alliances** in this paper and seven sub-groups or **associations**

(Appendix I). Two of the groups, the *Pericalymma-Hypocalymma* alliance, with two associations, and the *Pericalymma-Regelia* alliance, with three associations, contain the shrub *Pericalymma ellipticum* as one of the characteristic species. The other main wet heathland group, the *Melaleuca-Cassytha* alliance which is divided into two associations, does not contain *P. ellipticum* but is usually dominated by shrubs of *Melaleuca* spp., the most characteristic of which is *M. incana*. The climber *Cassytha glabella* is also a characteristic component of these heathlands. In general the *Pericalymma-Hypocalymma* alliance is found on deep sands (humus podzols), with organic depositional layers at 1 to 1.5 metres, north of the Capel River and the *Pericalymma-Regelia* alliance is found on a range of soils from deep sand to shallow loams, usually with a laterite hardpan at less than a metre, south of the Capel River. The *Melaleuca-Cassytha* alliance is found on deep clays or sand over clay north of the Capel River. The typical soils for each of the associations are summarized in Table 1.

Similarity of alliances, associations and quadrats

The Sorensen coefficients of community of the various alliances and associations are given in Table 2. This coefficient, which has a maximum value of 200 when the two samples being compared have all their species in common,

Table 1

Soil descriptions for wet heathland communities of the southern Swan Coastal Plain.

Association	Soil Description
Pericalymma-Hypocalymma alliance	
P. ellipticum-H. angustifolium-Hibbertia vaginata [A1]	Deep (> 1 m) light grey[1] sand sometimes with an organic deposition hardpan at 1 to 1.5 m. High organic matter content in A1 horizon [Uc 2.33][2]. Top soil[1]-C/N ratio: moderate-high (23-27), P (total): very low (20-30 ppm), pH: strongly acid (5.0-5.5)[3].
P. ellipticum-Evandra pauciflora-Hypolaena exsulca [A2]	Deep (> 1 m) light grey to greyish brown sand sometimes with an organic deposition or laterite hardpan at 1 to 1.5 m [Uc 2.31]. High organic matter content in A1 horizon. Top soil-C/N ratio: moderate-high (23-27), P (total): very low (20-30 ppm), pH: strongly acid (4.9-5.5).
Pericalymma-Regelia alliance	
P. ellipticum-R. ciliata-Leptocarpus canus [B1]	Pale brown, brown or grey sand to sandy loam over laterite hardpan at 0.25-1 m [Uc 2.21]. Top soil-C/N ratio: low-moderate (18-21), P (total): very low-low (40-70 ppm), pH: moderately acid (5.4-6.1).
P. ellipticum-Chamelaucium roycei-Grevillea diversifolia [B2]	Dark reddish brown loam to greyish brown or brown sandy loam over laterite hardpan at 0.1 to 0.5 m [Um 5.21/Uc 5.11]. Top soil-C/N ratio: low (16-18), P (total) very low to high (40-400 ppm), pH: moderately acid (5.4-5.9).
P. ellipticum-Kunzea recurva-Daviesia preissii [B3]	Deep (> 1 m) light grey fine sand to grey brown sandy loam over laterite caprock at 1 to 1.5 m [Uc 2.21]. High organic matter content in A1 horizon. Top soil-C/N ratio moderate to high (23-28), P (total) very low (40-50 ppm), pH moderately acid (5.5-5.9).
Melaleuca-Cassytha alliance	
M. viminea-Isolepis nodosa-C. glabella [C1]	Deep (>1 m) greyish brown to light yellowish brown heavy clay [Ug 5.14]. Top soil: C/N ratio very low-low (9-17), P (total) low-moderate (40-120 ppm), pH strongly-moderately acid (4.8-6.2).
M. incana-M. hamulosa-K. recurva [C2]	Deep (> 1 m) grey brown sand overlying very pale brown sandy clay [Uc 1.21]. Top soil: moderately acid (5.5-6.0), may have high salt content.

[1] Soil colour according to Munsell colour charts. [2] Northcote (1975) soil classification. [3] Soil chemical data from Pym & Poutsma (1957), McArthur & Bettenay (1956, 1958), McArthur (1991) and Smith 1994.

summarizes the similarity in composition of the species groups. Although structurally the three wet heathland alliances have the same variants (heathland-sedgeland, heathland and tall heathland), the similarity between alliances based on shared species is relatively low with Sorensen's coefficients of community between 16 and 22. This indicates a high degree of beta diversity despite quite low species richness. Even within alliances, the highest coefficient is 49 and it is generally lower than 32.

of the *Pericalymma-Hypocalymma* alliance. The third axis (not shown) divided the *P. ellipticum-R. ciliata-L. canus* and *P. ellipticum-K. recurva-D. preissii* association quadrats at one end (high values) from the *P. ellipticum-C. roycei-G. diversifolia* association (low values) with the *Pericalymma-Regelia* alliance quadrats occupying intermediate values. Unfortunately, because soil data were not recorded from each quadrat, it is not possible to more precisely relate values on the DCA axes to edaphic variables.

Table 2

Total species numbers and Sorenson coefficients of community of the wet heathland alliances and associations.

	A	B	C
Alliance			
A *Pericalymma-Hypocalymma* (56 spp.)	—	21.6	16.8
B *Pericalymma-Regelia* (120 spp.)		—	17.6
C *Melaleuca-Cassytha* (39 spp.)			—

	A1	A2	B1	B2	B3	C1	C2
Association							
A1 (33 spp.)	—	49.2	21.7	12.3	18.9	13.6	3.9
A2 (28 spp.)		—	21.0	7.9	23.2	14.8	4.3
B1 (96 spp.)			—	29.2	30.6	12.9	7.0
B2 (48 spp.)				—	18.0	8.1	6.1
B3 (41 spp.)					—	14.9	10.2
C1 (26 spp.)						—	31.8
C2 (18 spp.)							—

The eigenvalues of the first four axes of the DCA were 0.74, 0.39, 0.29 and 0.22. The DCA clearly divided the 47 quadrats into the three major alliances and reinforced the outcome of the classification (Fig 2). It also confirmed the greater similarity of the *Pericalymma-Hypocalymma* and *Pericalymma-Regelia* alliances to each other than each has with the *Melaleuca-Cassytha* alliance. The values along the major axes appear to be related to the soil types at the wet heathland sites. The highest values on axis 1 correspond with the deep clays of the Wellard and Byrd Swamp nature reserves, with slightly lower values associated with the deep sands over clay at Hay Park. Low values on both axis 1 and axis 2 are associated with the shallow sandy loams and loams of the Tutunup-Ruabon area. An increase in value on axis 2 appears to correspond with an increase in soil depth and increasing sandiness of the soil, with the highest values occurring at reserve ↑1167 which has deep grey sands, but which also has a higher cover of sedges than the other sites
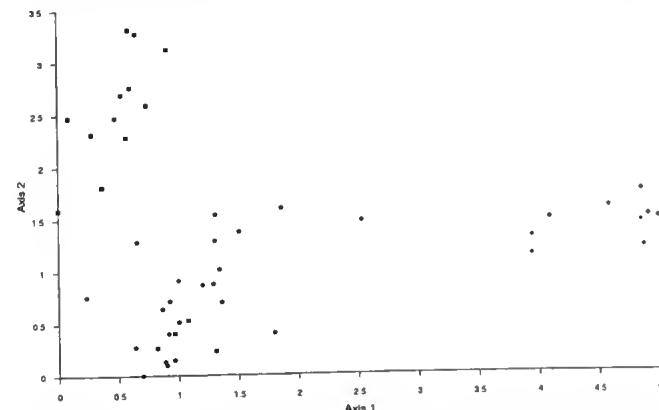
Figure 2. Detrended Correspondence Analysis ordination (axes 1 & 2) of 47 wet heathland quadrats from the southern Swan Coastal Plain showing the three alliances derived from the TWINSPAN classification. ■ *Pericalymma-Hypocalymma* alliance, • *Pericalymma-Regelia* alliance, ◆ *Melaleuca-Cassytha* alliance.

Description of associations

The *Pericalymma-Hypocalymma* alliance. The *P. ellipticum-Hypocalymma angustifolium-Hibbertia vaginata* association (association A1 in Appendix 1, Table 1) is found on the deep acid grey sands (Joel series and related Swamp types) of the Bassendean Association (Pym & Poutsma 1957) in the northern part of the study area. These soils have an organic B horizon, which may be concreted to form a hardpan, at 1 to 1.5 metres. It is probably the most extensive of the wet heathland formations on the southern SCP being found in State Forest on the east side of the McLarty and Myalup Plantations and in nature reserves in the Kemerton area. The wetlands in which this heathland association are found occur as regularly spaced depressions, or interdune swales, and are classed as sumplands (seasonally inundated basins) of the Riverdale suite by Semeniuk (1988). Recharge of the sumplands is by precipitation or groundwater rise. Structurally, the association is mid-dense to closed heathland (Walker 1983) dominated by shrubs up to about 1 m with varying amounts of graminoids up to about 25% of ground cover and in some places emergent *Xanthorrhoea preissii, Melaleuca preissiana* or *Nuytsia floribunda*. The heathlands grade into *Eucalyptus marginata-E. calophylla* open forest on low sandy rises, *M. rhaphiophylla* and *M. preissiana* low forest in wetter areas, and *E. gomphocephala-E. marginata* forest on the sands of the Karrakatta Association to the west.

The *P. ellipticum-Evandra pauciflora-H. exsulca* association (A2) is found on similar soils and topographical positions to the association described above, and they have many species in common. The main difference is the greater dominance of *P. ellipticum* and the larger proportion of the Cyperaceae and Restionaceae in the *P. ellipticum-E. pauciflora-H. exsulca* association which may indicate that the sites are somewhat wetter. This association is found in State Forest west of

Harvey, and on several small reserves in the same area and also south of Bunbury. In the Harvey area, the soils are of the Joel series and related types of the Bassendean Association, and in the Bunbury-Capel area they are the Swamp series VI of the Southern River Association (McArthur and Bettenay 1956). The presence of organic or ferruginous hardpans at about 1 metre as found in some of these soils may account for the increased proportion of graminoids characteristic of this association. Structurally, the association is a mid-dense to closed heathland, generally below 1.2 metres tall, with occasional emergent *Kunzea ericifolia* or *M. preissiana*. It may grade into a low forest of *M. preissiana* or a sedgeland dominated by *E. pauciflora* in wetter areas and into *E. marginata-E. calophylla* forest or *K. ericifolia* tall shrubland or *Banksia attenuata* woodland on interswale dunes.

The **Pericalymma-Regelia** alliance. The *P. ellipticum-Regelia ciliata-Leptocarpus canus* association (B1) is the most widespread group within this alliance, being found on the Wet Sand soil type of the Abba Wet Ironstone Flats land unit (Tille & Lantzke 1990). These acid grey sands are similar to the Joel Sand of the Bassendean Association and have a similar origin. They may grade into the Bog Iron Ore Sand of Tille and Lantzke (1990) when the laterite hardpan comes to within less than 50 cm of the surface. The heathlands of this association occupy a similar position topographically to the Joel Sand of the Bassendean Association being found in shallow depressions and swales in areas of sandplain and low dune fields. The association is restricted to road verges and three small (<200 ha) nature reserves between Tutunup and Ambergate south of Busselton. The structure of the mature formation is mid-dense to closed heathland which varies in average height from 0.6 to 1.2 m but may be up to 1.6-1.8 m (tall heathland) in some areas. The species richness of the shorter heathland, particularly that at the Ruabon Nature Reserve and part of the Fish Road Nature Reserve, is only about half of that of the taller heathland. In other areas, with deeper soils, species characteristic of the association such as *Melaleuca uncinata, M. hamulosa, Hakea varia, R. ciliata* may grow to more than 2 metres high. At Tutunup the association merges quite sharply with *E. calophylla* forest, which has an almost completely different suite of species in the understorey, and is situated on the low rises interspersed with the heathlands. The soils on these rises are deep (1.5-2.0 m) Abba and Busselton sands (Tille & Lantzke 1990).

The *P. ellipticum-Chamelaucium roycei-Grevillea diversifolia* association (B2) is perhaps the most restricted unit in the *Pericalymma-Regelia* alliance. It is confined to shallow loams over laterite hardpan along a road and rail reserve in the Tutunup area southeast of Busselton and covers less than 10 hectares. The soils are the Bog Iron Ore Loams of the Abba Wet Ironstone Flats land unit (Tille & Lantzke 1990) with less than 30 cm of brown loam overlying a massive laterite hardpan. This association merges with the *P. ellipticum-R. ciliata-L. canus* association which occurs where the laterite is deeper than about 30 cm and the loam gives way to loamy sand and sand. It is wetter than the latter association and sometimes water stands several centimetres deep above the soil surface over the winter months. The drainage along the verge has been modified by road and railway construction, the latter taking place over 120 years ago. The declared endangered species *C. roycei* is characteristic of this association. Several undescribed taxa including species of *Loxocarya*,

Restio and *Dryandra* are also found. Structurally the association is closed heathland to tall closed heathland (Walker 1983) with emergent *Viminaria denudata, Xanthorrhoea preissii,* and various *Melaleuca* species up to 3 m high.

The *P. ellipticum-Kunzea recurva-Daviesia preissii* association (B3) differs from the other two associations within the alliance mainly in regard to the taxa that it does not have. *Regelia ciliata* is replaced by a similar myrtaceous shrub *Kunzea recurva* and it does not have the rich cover of species in the genera *Lepyrodia, Leptocarpus, Restio* and *Loxocarya* found in the other associations. It also has a restricted distribution, being found at Ambergate and Yoongarillup on small nature reserves. At Ambergate the soils are of the Wet Sand or Busselton type (Tille & Lantzke 1990) with laterite hardpan at about 1 m, at Yoongarillup the soils are brown sandy loams over sandy clay loams (Mixed Alluvial Soils; Tille & Lantzke 1990). The *P. ellipticum-K. recurva-D. preissii* association is also a mid-dense to closed heathland with occasional emergent *X. preissii*, grading into *E. marginata-E. calophylla* forest on the slight rises surrounding the shallow depressions in which the heathland is found.

The **Melaleuca-Cassytha** alliance. The *Melaleuca viminea-Isolepis nodosa-Cassytha glabella* association (C1) is found in the northern part of the study area on small remnants of uncleared heavy kaolinitic clays of the Serpentine River soil association (Pym & Poutsma 1957). The very low permeability of these clays and the level topography restricts drainage and water lies on the surface for several months over winter. They occur near the boundary between the Bassendean Dunes and the alluvial Pinjarra Plain and the soils were formed by the build-up of alluvium from streams terminating in the Bassendean Dunes (Semeniuk 1988). It forms a closed heathland at the Wellard Reserve and a tall heathland (1.5-2.5 m) at Byrd Swamp Reserve, with up to half of the ground cover being provided by sedges and restiads (*Isolepis, Lepyrodia, Leptocarpus, Gahnia*) in some areas. Climbers, primarily *C. glabella*, are also prominent. On the low sandhills surrounding the heathland association occurs *Agonis flexuosa* or *Kunzea ericifolia* low forest or *E. marginata-E. calophylla* forest with an understorey of Banksia species. In wetter areas *M. rhaphiophylla* low forest with an understorey including *M. lateritia, Astartea fascicularis* and *Lepidosperma longitudinale* may be found.

Further south, near Bunbury, the *Melaleuca incana-M. hamulosa-Kunzea recurva* association occurs on deep grey sand over sandy clay. This soil is similar to the Stirling VII Sand and Swamp Series IV of McArthur & Bettenay (1956). Although it is also alluvial in origin, it is much more permeable than the clays of the *M. viminea-I. nodosa-C. glabella* association, however during winter the watertable may rise above the ground surface. This association is represented by only one site, within the city of Bunbury, although it probably occurs in other areas south of Bunbury near the junction of the Bassendean and Spearwood dune systems. It is similar structurally to the tall heathland variant of the *M. viminea-I. nodosa-C. glabella* association found at Byrd Swamp but with the sedge *Gahnia trifida* and the native grass *Sporobolus virginicus* forming the graminoid component rather than *Isolepis* and *Lepyrodia* species. On better drained soil to the east of the heathland occurs a low woodland of *Melaleuca preissiana*.

Discussion

Comparisons with other heathlands: Species richness

The *Pericalymma-Regelia* and *Pericalymma-Hypocalymma* wet heathland alliances of the southern Swan Coastal Plain have a comparable species richness to similar communities in New South Wales and Queensland. At the 100 m² scale, wet heathland in Royal National Park and Ku-ring-gai Chase near Sydney averaged 23.9 and 18.0 species respectively (Specht & Specht 1989) compared to 15.8 (up to 21 / 100 m²) for the *Pericalymma-Hypocalymma* alliance and 18.4 (up to 26 / 100 m²) for the *Pericalymma-Regelia* alliance. However the southern SCP alliances are considerably less species rich than other coastal heathlands on sand in Western Australia. At Nornalup National Park, wet heathlands growing on similar soils had 34 species per 50 m² (George *et al.* 1979) and at Scott River a low open heathland on deep grey sand had 40 species per 100 m² (Specht & Specht 1989). The low species richness of the *Melaleuca-Cassytha* alliance and of some of the wetter areas of the other two southern SCP communities (9-12 species / 100 m²) is similar to that of the species poor heathlands of northern Europe (Gimingham *et al.* 1979).

Comparisons with other heathlands: Floristics

There are few published reports of the floristics of other wet heathlands in Western Australia, and none of these has attempted a classification of this community type. Wardell-Johnson *et al.* (1989) describe two wet heathland communities growing on humus podzols over deep sands at Nornalup near the south coast of Western Australia, called the *Beaufortia sparsa* plain and *Dasypogon bromeliifolius* heathland communities. These communities share *Adenanthos obovatus, Lysinema ciliatum, Melaleuca thymoides,* and *D. bromeliifolius* with the *Pericalymma-Hypocalymma* alliance. Havel (1968) describes a low *M. preissiana* woodland growing within the Bassendean Dune system near Perth. Apart from *M. preissiana,* this community has *P. ellipticum, A. obovatus, D. bromeliifolius* and *H. angustifolium* in common with the *Pericalymma-Hypocalymma* alliance. Keighery & Trudgeon (1992) describe several wet heathland communities growing on the SCP near Perth, which are dominated by *P. ellipticum* and which, in common with the *Pericalymma-Regelia* alliance, include *P. ellipticum, Hakea sulcata, Xanthorrhoea preissii, Stirlingia latifolia, Calothamnus lateralis* and the sedges *Mesomelaena tetragona* and *Hypolaena exsulca.* Keighery & Robinson (1990) mention wet heathlands growing on red clays and loams over laterite hardpan on the Scott Plains east of Augusta, which share a number of rare taxa with the *Pericalymma-Regelia* alliance. The *Melaleuca-Cassytha* wet heathland alliance has taxonomic affinities with low woodlands and low closed forests dominated by *M. rhaphiophylla* and *M. cuticularis* around swamps and on seasonally wet areas of the Yoongarillup Plain landform south of Perth (Trudgeon 1991; R Smith *pers. obs.*).

The remnant wet heathlands growing on the northern part of the SCP and on the Scott Plains are apparently species rich, and the bulk of the taxa occurring in them are different from those in the communities which were the subject of this study. There is a clear need for a formal classification of these communities because they are threatened by urban development and mining (Keighery & Robinson 1990; Gibson & Keighery 1992).

A comparison of the most important plant families within each of the southern SCP wet heathland alliances (Table 3) shows a very high proportion of Myrtaceae in the *Melaleuca-Cassytha* alliance. The percentage of Restionaceae in the *Pericalymma-Hypocalymma* and *Pericalymma-Regelia* alliances is about double that of the 25 mostly dry heathland sites surveyed in the south west of Western Australia by George *et al.* (1979). Except for the *Pericalymma-Regelia* alliance, the proportion of Proteaceae in the SCP heathlands is lower than most Western Australian dry heathlands (George *et al.* 1979; Brown & Hopkins 1983) where it is generally above 15%. As with most Australian heathlands, there was a low proportion of species of the Epacridaceae in the flora of the southern SCP heathlands and where they did occur they had low foliage cover values. This is in contrast to the wet heathlands of Europe and South Africa where the closely related family Ericaceae is often a dominant component of the community (Gimingham *et al.* 1979; Cowling & Holmes 1992).

Table 3

Numbers and percentage (in brackets) of species in each of the major plant families in the southern Swan Coastal Plain wet heathlands. Only those species which were positively identified have been included.

Family	*Pericalymma-Hypocalymma*	*Pericalymma-Regelia*	*Melaleuca-Cassytha*
Myrtaceae	8 (15%)	11 (12%)	11 (31%)
Proteaceae	3 (6%)	15 (21%)	3 (8%)
Leguminosae	7 (14%)	8 (8%)	5 (14%)
Restionaceae	6 (12%)	11 (12%)	3 (8%)
Cyperaceae	3 (6%)	3 (3%)	4 (11%)
Liliaceae	4 (8%)	5 (5%)	1 (3%)
Epacridaceae	3 (6%)	1 (1%)	-
Stylideaceae	1 (2%)	5 (5%)	-
Dilleneaceae	2 (4%)	4 (4%)	-
Droseraceae	2 (4%)	3 (3%)	1 (3%)
Orchidaceae	2 (4%)	-	3 (8%)

Ecological processes

Only some general comments can be made on ecological processes within the wet heathlands of the SCP as there has been little ecological research in these communities. Clearly the soil moisture regime is critical in determining the extent of the wet heathland formation and in modifying plant species composition within the formation. The *Pericalymma-Hypocalymma* and *Pericalymma-Regelia* alliances are similar to the groundwater heaths described for eastern Australia by Groves & Specht (1965) and Siddiqi *et al.* (1972) which are subjected to extremes in soil moisture availability. In the rainy season the watertable is close to the surface for several months, while during the dry season the soil above the impermeable layer of clay, peat, or laterite hardpan underlain by clay, drys out. As plant roots are generally not able to penetrate this layer, water deficits become severe in summer. The rapid drying out of these soils was illustrated by a study of watertable levels along a transect from heathland on shallow loam over laterite hardpan to woodland on deep sands at Tutunup (Smith 1994). In late August and early September, the watertable was 3 cm to 5 cm above the surface in the heathland and 5 cm to 14 cm below the surface in the woodland. By late October the watertable in the heathland had withdrawn to within or below the laterite (50 cm below the surface) and in the woodland the watertable was greater than 85 cm below the surface.

As well as the stress caused by the drying out of the relatively shallow soils in summer, high watertables in winter cause additional stress to the heathland species. Waterlogging by perched watertables causes soil air, which is essential to root respiration, to be expelled from the soil (Specht 1981). The duration of waterlogging is important in determing the species composition of wet heathlands (Webster 1962; Siddiqi *et al.* 1972). The seedlings of many sclerophyllous trees are very sensitive to prolonged waterlogging (> 2-3 months) and thus fail to establish in adjacent heathland soils whereas the seedlings of heathland plants generally have morphological or physiological adaptations which alleviate the anaerobic conditions (Specht 1981).

Few nitrifying or nitrogen-fixing bacteria can exist under the poorly aerated conditions of waterlogged soils (Woolhouse 1981) and therefore these soils may be low in available N. Inhibition of the nitrification process (Groves 1981) is indicated by the high C/N ratios (23-27) of the podzols of the *Pericalymma-Hypocalymma* alliance (Table 2). Leaching of the soils in wet heathlands may also lead to a reduction in some cations, notably Ca^{2+}, Mg^{2+} and K^+. Research into the ecology of European wet heathlands has shown that nutrient-poor, waterlogged sites act as refugia for slow growing plants which are not able to compete well on better aerated, fertile soils (Berendse & Aerts 1984).

A comparison of soil nutrients in the Bog Iron Ore and Wet Sand soils under wet heathland at Tutunup with those in the Abba Sand under *Eucalyptus marginata-E. calophylla* forest adjacent to them shows the heathland soils to have similar levels of total N and total P, higher extractable K and Na but substantially lower extractable Ca and Al (Smith 1994). Some of the Bog Iron Ore loams have quite high levels of total P (up to 400 ppm) but this nutrient is probably strongly bound by iron oxides and extractable P is low

(McArthur 1991). The low total P concentrations of most of the wet heathland soils of the southern SCP (Table 2) are typical of Australian heathlands (Groves 1981; Keith & Myerscough 1993).

Disturbance in the wet heathlands

Most of the wet heathlands surveyed in this study occur on reserves of less than 200 ha or on narrow road reserves, and are surrounded by cleared agricultural land or pine plantations. Fragmentation of these areas of natural vegetation may have major effects on various ecological processes, such as the water and nutrient cycles, and especially in the smaller fragments, the radiation balance and wind regimes (Hobbs 1993). Clearing of the surrounding native vegetation may lead to a rise in the watertable and consequent salt accumulation near the surface, as has occurred on the lower SCP since at least the 1950's (McArthur & Bettenay 1956). Fertilizer drift from adjacent farmland may disrupt the natural nutrient cycle and encourage the invasion of exotic plants (Smith 1990).

Too frequent fire is another stress which may lead to the deterioration of natural vegetation in ecosystem fragments. Although most of the sites surveyed for this study had apparently not been burnt for 8-10 years, much of the heathland along the Tutunup-Ruabon railway was recently burnt, and was burnt for fuel reduction every few years in the past (F Negus *personal communication*). The vegetation of the wet heathlands recovers quite rapidly after fire due to the high proportion of resprouters (R Smith *personal observation*). However the post fire environment with its abundant light and increased nutrient levels in the ash bed provides an ideal seed bed for invasive weed species which may out-compete slower growing native species (Baird 1977). The combination of recurrent fire and rising salinity levels may place extra stress on the recovery of species which normally require establishment of seedlings after fire (Baird 1984).

This survey provides a systematic analysis of a community which is likely to be one of the rarer components of the Western Australian vegetation. If biodiversity is to be an important criterion for conservation of this vegetation type in this State, then the high species turnover (beta diversity) of the heathlands needs to be taken into account. Several of the sites surveyed for this study are not in conservation reserves, in particular the highly diverse heathlands of the Tutunup area. To preserve what is left of the diversity of this ecosystem, all of the sites included in this study need to be in conservation reserves where they can be more easily managed. More detailed work needs to be completed on the northern part of the coastal plain and along the south coast to provide a complete picture of the wet heathlands of Western Australia.

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Appendix 1. Two-way table produced by TWINSPAN classification of 47 southern Swan Coastal Plain wet heathland quadrats. Underlined species names are the characteristic species of the alliances and associations. Values shown within the table are the Braun-Blanquet cover values for the species. Only species occurring in more than two quadrats are included.

Quadrats — Alliances and Associations:

- **Pericalymma-Hypocalymma**
  - A1: 27 29 33 34 35
  - A2: 46 47 28 45 39 40 41
- **Pericalymma-Regelia**
  - B1: 8 7 10 12 13 14 11 15 18 17 19 20 16 21 22 1 2
  - B2: 3 4 5 6 9
  - B3: 23 36 37 38
- **Melaleuca-Cassytha**
  - C1: 24 30 31 32 25 26
  - C2: 42 43 44

Species	27	29	33	34	35	46	47	28	45	39	40	41	8	7	10	12	13	14	11	15	18	17	19	20	16	21	22	1	2	3	4	5	6	9	23	36	37	38	24	30	31	32	25	26	42	43	44
Conostylis serrulata																							1	1		1	1																				1
Phylidrella pygmaea																		1	1																										1		
*Parentucellia viscosa													1																		1		1												1		
Acacia stenoptera														1	1	1	1																														
Chamelaucium roycei													1	1					1										1	1	2	2	2	1													
Grevillea diversifolia													2	1									1						1	2	2	2	3														
Leptocarpus aristatus																							1							3	2	2	2														
Loxocarya aff. flexuosa																					1										2	3					2										
*Briza maxima																				1											1	1					1										
Hakea ceratophylla																				1	2	1	2			2	2								1												
Hakea sulcata														1			1		1	1	2	1	1			1	1								1												
Isopogon formosus													2	1	2		2		1				1	2		1									1												
Regelia ciliata													4		3		3	1	2	2	3		2	3	3	4	1		2	1	2	1				3	3										
Leptocarpus canus													1	2	2	2	2	1	2	2	2						1			2	1																
Leptocarpus elegans															2	1	2		1			1	1				1	1									2										
Melaleuca uncinata														1				1			1	1																1									
Conostylis aculeata																	1		1	1	1	1							1	2																	
Xanthorrhoea gracilis	1	1																			1			1		1	1	1		1					1	1											
Allocasuarina humilus																	1	1	1										1						1							1		1			
Calothamnus lateralis					1								2								1	1	2	1						1							1		1		1	1	1				
Dryandra nivea													1	1	1	2		1	1				1	1						1							1		1		1	1	1	1			
Grevillea brachystylis																					1			1	1					1					1												
Helichrysum cotula													1								1			1						1								1									
Loxocarya fascicularis													1				2		1								1			1								1									
Stirlingia latifolia															1		2		1		2			1		2	2						1		2		1										
Hibbertia rhadinopoda													1																		2				2									1			
Mesomelaena tetragona														1	1		1			2			1		1	2	1			1					2		1	4									
Synaphea reticulata														1		1	1		1																2		1	1									
Tricoryne eliator													1				1																				1	1									
Daviesia preissii												1																							1	1	2	1									
Boronia dichotoma						1	1		1				1										1	1			1								1		1	1									
Acacia pulchella		1			1	1	1						1													1	1			1					1		1	1									
Pericalymma ellipticum		1			1	4	4	3	3	4	4	3	1	4	2	4	4	3	4	4	4	4	3		2	4	4	4	4	4	4	4	4	3	4	3	2	1									
Xanthorrhoea preissii			1	1	2	1	1		1				1	1	2	2		2						1		1	1							1	1	1	1	1									
Adenanthos meisneri	2		1	1	1	1	1		2			1	1	1	2	2	1	1					2			1	1	1	1										1								
Dampiera linearis	1		1	1			1	1	1				1			1			1	1			1	1	1	1			1						1		1			1				1			
Acacia flagelliformis										1	1	1			1	1												1	1																		
Evandra pauciflora	1					1	1		3	3	1	2																																			
Acacia semitrullata		1	1	1		1	1		1						1																																
Adenanthos obovatus	1	1	1	1	1	2	1	1	1																1	2		1							1									1			
Dasypogon bromeliifolius	1	2	1	2	3	2	2	2	2																																						
Euchilopsis linearis	1	1	1	1		2	1	1	1	1																		1																			
Hypocalymma angustifolium	3	2		2	2	2	2	1	2	1	2	2														2	2								1												
Kunzea ericifolia	1				1	1	1		2	1																																					
Lysinema ciliatum			1							1	2					1														1																	
Hibbertia vaginata	1		1	1	1							1				1																															
*Hypochaeris glabra		1	1	1																													1														
Lyginia barbata		1	1	1	2																			1												1	1										
Lepidosperma angustatum				1																			1										1										1				
Hypolaena exsulca		1				1	1	1	1	1	1	2			1	1			1	1							1	1							1					2	2						
*Ursinia anthemoides	1	1	1	1	1																																		1						1		
Melaleuca preissiana						1	1		1																																		1				
Drosera macrantha													1															1		1					1	3	2		1				1		1	1	2
Hakea varia																					2	3	1				1		1						1	3	2		1					1	1	1	2
Sphaerolobium medium																				1	1	1	1	1			1		1							1	1	1	1	1	1	1		1			1
Acacia saligna																														1		1	1				1									1	1
Kunzea recurva																																1	1			3	1	4				1	1	2	2	1
Thysanotus patersonii			1	1		1																																1			1						
Lepyrodia glauca																													1		1								2		1	2					
Hakea marginata																																								1	1	1	1	1			
Lepyrodia muirii																																							4	4	3	2					
Melaleuca viminea																																							2	4	3	2	3	3			
Isolepis nodosus																																							1	1	2	2	2	1		2	1
Cassytha glabella									1					1						1			1	1									1	1					1	1	2	2	2	1	2	2	3
Melaleuca incana																																											2	2	2	1	1
Gahnia trifida																																											1		2	1	1
Sporobolus virginicus																																													1	2	1
Melaleuca hamulosa													1													1	1	2																	3	2	2

*Exotic species

Seed dispersal of *Hibbertia hypericoides* (Dilleniaceae) by ants

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Abstract

The "Yellow Buttercup", *Hibbertia hypericoides* occurs abundantly in association with several different vegetational types in the south west of Western Australia. In remnant urban bushland at Perth, Western Australia, seeds are collected by two *Melophorus* species, *Rhytidoponera violacea* (Forel) and *Iridomyrmex discors* (Forel). In banksia low woodland at Cooljarloo, a species of the *Iridomyrmex rufoniger* group and *Rhytidoponera violacea* (Forel) collect seeds of *H. hypericoides*. One of the *Melophorus* species discriminates between potentially viable seeds, which are enclosed by a pulpy aril and non-viable seeds which show only a thin, short aril. Large numbers of potentially viable seeds are collected; the aril is consumed and the seeds discarded in the refuse heaps of the colony. The aril is rich in lipids, and the most common fatty acid in both seed and aril is oleic acid. Preliminary laboratory experiments indicate that seed germination is similar in sand collected around ant nests and sand collected elsewhere in the same habitat.

INTRODUCTION

Many Australian native plants produce seeds with fleshy and highly nutritious appendages, called food bodies or elaiosomes (Sernander 1906; Berg 1975). In numerous plants these are the arils, structures growing from some part of the ovule, or funicle, after fertilization (Corner 1976; Takhtajan 1991). Ants, attracted to the elaiosome, may carry the whole diaspore (seed plus elaiosome) to their nest and consume the food body but leave the seed intact. Such seed dispersal is called myrmecochory. In contrast, seed harvesting (granivorous) ants destroy the whole diaspore (Berg 1975; Majer & Lamont 1985; Andersen 1990; Majer 1990; Hughes & Westoby 1992a).

Myrmecochory is particularly common in the dry sclerophyll vegetation of Australia (Berg 1975; Davidson & Morton 1981a,b; Rice & Westoby 1981) and South Africa (Milewski & Bond 1982). Plants are assumed to benefit from seed dispersal by ants since seeds may be carried to more advantageous germination sites (Handel 1976; Davidson & Morton 1981a,b; but see Drake 1981; Hughes & Westoby 1992a). Seeds that have been handled by ants may also germinate better (Horvitz 1981). Furthermore, seed dispersal by ants may allow colonisation of more distant habitats, and dispersed seedlings may escape competition from parent plants and siblings (Berg 1975). Finally, seeds inside the ant nest may be protected from fire (Berg 1975) and predators (Heithaus 1981). The ants, in return, benefit from their myrmecochorous behaviour since the elaiosome is rich in lipids and vitamins (Bresinsky 1963; Beattie 1985; Oostermeijer 1989; Hughes & Westoby 1992b).

Viable seeds of *Hibbertia* (Dilleniaceae) are partly or completely enclosed by a pulpy aril. Ants are important dispersal agents of seeds of *H. vestitata, H. obtusifolia* and *H. ovata* (Drake 1981; Berg 1975; Hughes & Westoby 1992b) in Eastern Australia, and it has been shown for *Hibbertia ovata* that the aril functions as an elaiosome (Hughes & Westoby 1992b). The only observations on seed dispersal for Western Australian *Hibbertia* species are for *H. cuneiformis*. Seeds of this species are enclosed by a pulpy, bright orange aril and are collected by birds (N Marchant, quoted in Stebbins & Hoogland 1976).

Hibbertia hypericoides, the "Yellow Buttercup" is widespread in low banksia woodlands from Augusta to Northhampton, Western Australia (Wheeler 1987), and often dominates the understorey of a site. Mature seeds are either brown, red or black. Brown and red seeds have a short transparent aril, but black seeds are almost fully enclosed by a white, pulpy aril. Black seeds contain firm, white endosperm, but brown and red seeds are characterized by shrivelled or no endosperm. Hence only black seeds are potentially viable. Initial observations indicate that ants collect the seeds of *H. hypericoides* soon after they have dropped to the ground.

Here we describe seed collecting ants and the amount and type of seeds taken, and examine the following hypotheses: (1) ants collect potentially viable seeds more often than non-viable seeds, (2) the aril is rich in lipids, (3) ants are attracted to the aril, and (4) germination of seeds as well as survival and growth of seedlings is higher in ant nests than elsewhere in the same habitat.

METHODS

Study sites and voucher deposition

Field study sites were in Kings Park and Wireless Hill Park, both within the Perth metropolitan area, Western Australia (115°50' E, 31°56' S), and Cooljarloo, *ca*. 200 km north of Perth near Cataby (115°35' E, 32°0' S). The natural bushland of Kings Park and Wireless Hill Park is character-

ized by low banksia-sheoak woodland (*Banksia attenuata, B. menziesii, Allocasuarina fraseriana, A. humilis*) with jarrah (*Eucalyptus marginata*) and marri (*E. calophylla*) interspersed. *Hibbertia hypericoides* dominates the understorey, with individual plants on average between 3 and 5 m apart. Other common understorey plants are *Macrozamia riedlei, Xanthorrhoea preissii, Stirlingia latifolia, Hypocalymma robustum* and *Jacksonia sternbergiana*. The natural bushland at Cataby is open low banksia-sheoak woodland interspersed with various *Melaleuca* species, *Conospermum stoechadis* and *Hypocalymma robustum*.

Plants with ripe fruits were visited in Kings Park, Wireless Hill Park and at Cooljarloo in December 1990. Seed collecting ants were recorded and sampled for subsequent identification. Voucher specimens are held in a reference collection at the School of Biology, Curtin University or in the Australian National Insect Collection. When species names were unavailable they are either identified with Curtin University code numbers (JDM) or, if voucher specimens are deposited there, with Australian National Insect Collection codes (ANIC).

Seed yield

During December 1990 a total of 40 nests of the most significant seed collecting ant species were visited in Kings Park and Wireless Hill Park. At Cooljarloo 16 nests were visited. The numbers and types of *H. hypericoides* seeds in the refuse heaps were counted, then the upper 30 cm of the soil layer of each nest was removed in order to determine the number and type of seeds inside the nest (Shea *et al.* 1979 found no seeds buried deeper than 30 cm by ants of *Melophorus* sp. 1 (ANIC) in the southern jarrah forest). The distance between each ant nest and the nearest *H. hypericoides* plant was recorded.

Lipid content of seed and aril

Since the nutritional value of seed and aril is mainly due to lipids, a chemical analysis was carried out in order determine the lipid content of seed and aril in *H. hypericoides*. Diaspores (black seeds with pulpy aril) were collected in December 1990 in the Perth metropolitan area, and the aril was removed. Seventy five mg of both arils and seeds were analysed for lipids.

Samples were homogenised with 2 ml of isopropanol; 3 ml of hexane was then added to each sample, and the mixtures allowed to stand for 12 h at room temperature. The supernatants were removed and the residues re-extracted using the same procedure. Supernatants were pooled for each sample and evaporated either under vacuum or with nitrogen. The residues, which contained the "lipid fraction", were weighed to establish the yield.

Lipid fractions (10-50 mg) dissolved in toluene were subjected to a methylation process by adding 4 ml of 1% sulphuric acid in methanol and allowing to stand for 12 h at 50°C. Five ml of 5% aequeous sodium chloride solution was added to each sample, followed by 5 ml of hexane. The mixtures were thoroughfully shaken and allowed to separate. The supernatant from each mixture was removed and the residue re-extracted with an additional 5 ml of hexane. Supernatants for each sample were pooled and then passed through a column of anhydrous sodium sulphate. These methylated lipid fractions in hexane were used for gas-chromatograph/mass-spectrograph analyses.

The methylated lipid fractions, which contained methylated fatty acids (FAMES) were analysed using an Hewlett Packard GC-MS (Model 5971). Chromatography was performed with an Econocap^R Carbowax 20M column (ID 0.32 mm and film thickness 0.25 μ) using helium as the carrier gas. The initial column temperature was 50°C for 5 min, followed by an increasing gradient of 5°C min^{-1} to a temperature of 240°C, with the latter temperature being held for at least another 20 min. Run times were approximately one hour. FAMES were identified by using known retention times of standards, and mass spectra.

Attractiveness of the aril

A choice experiment was conducted to determine if the aril is the main attractant to ants of *Melophorus* sp.1. Fifteen of their nests were randomly selected in Kings Park in December 1990. Three seeds, one black and shiny seed with a pulpy aril, one brown seed with a short, brittle aril, and one black seed without an aril (the aril had been removed with forceps), were placed 50 cm away from each nest. Ant behaviour towards these seeds was observed in terms of the time ants spent attending the seeds, whether the aril was consumed and whether the seeds were carried into the nest. All observations were made from 10 am to 1 pm, when temperatures were above 25°C.

Effect of soil on germination

The following experiment was performed in order to test whether the soil inside ant nests is beneficial to the germination of *H. hypericoides* seeds. Freshly collected (in 1990) black seeds were air dried for 3 weeks at room temperature and then planted in sand trays. Sand was collected from the natural habitat in Kings Park. Sand was taken randomly (from any open area which was not close to an ant nest), from underneath *H. hypericoides* bushes, and from ant nests of *Melophorus* sp. JDM 358. Sterilized coarse river sand was used as a fourth treatment. Between 3 and 6 sand trays were prepared with each of the four soil types, twenty five seeds placed in each. All trays were prepared at the end of December 1990 and left unwatered in the glass house of the School of Environmental Biology until the 20th of March 1991, when watering commenced. Surface soil temperatures from December to February ranged from 30 to 45°C during the day. The number of germinating seeds was counted every second day until the 30th of September 1991, when watering ceased. Watering of the trays re-commenced in March 1992, and the number of germinating seeds was counted regularly until the beginning of September 1992.

Survival of seedlings in the field

In Kings Park and Wireless Hill Park, plants and ant nests were scrutinised for seedlings in December 1991. Seedlings were tagged with flagging tape, re-visited in June 1992, and the number of surviving seedlings was recorded.

RESULTS

Ants as seed collectors

Ant species observed collecting seeds of *H. hypericoides* in the study sites belong to the genera *Melophorus* (Family Formicinae), *Rhytidoponera* (Fam. Ponerinae) and *Iridomyrmex*

(Fam. Dolichoderinae). *Melophorus* sp. JDM 358 was the main collector of *H. hypericoides* seed in Kings Park and Wireless Hill Park in 1990 (Table 1). Other ants taking seeds of *H. hypericoides* are *Melophorus* sp. 1 (ANIC), *Iridomyrmex discors* (Forel) and *Rhytidoponera violacea* (Forel). At Cooljarloo, *Rhytidoponera violacea* (Forel) and a species of the *Iridomyrmex rufoniger* group removed seeds of *H. hypericoides* (Table 1).

Attractiveness of the aril

The aril of potentially viable seeds of *H. hypericoides* functions as an elaiosome. *Melophorus* sp. JDM 358 is attracted to the aril of potentially viable seeds. Ants either take black seeds which are enclosed by an aril to the nest immediately or consume the aril first and then take the seeds back to the nest. Seeds without arils attached are less frequently

Table 1

Frequency with which different ant species collected seed of *H. hypericoides* as a percentage of the total number of observations (N) in three study sites in December 1990. Dashes: species was not observed in study site.

Site	N	*Melophorus* sp. JDM 358	*Melophorus* sp. 1 (ANIC)	*R. violacea*	*I. discors*	*I. rufoniger* group
Kings Park	63	70	20	5	5	–
Wireless Hill	32	100	–	–	–	–
Cooljarloo	16	–	–	70	–	30

Nests of *Melophorus* sp. JDM 358 are abundant in Kings Park and Wireless Hill Park and are on average 1.24 m (n = 24) and 1.5 m (n = 36) respectively from the nearest *Hibbertia* plant. At Cooljarloo, nests of *Rhytidoponera violacea* are on average 1.2 m from the nearest *H. hypericoides* plant (n = 16). In the Perth metropolitan area, *Melophorus* sp.1 (ANIC) and *Melophorus* sp. JDM 358 start building (or re-open) nests from the previous season in September. They collect large numbers of *Hibbertia* petals which are carried inside the nest and subsequently discarded outside the nest on refuse heaps or middens, hours or days later. Ants begin to collect seeds at the end of October and continue until December when the last seeds mature.

Seed yield

Seed numbers were determined in nests of *Melophorus* sp.1 (ANIC) and *Melophorus* sp. JDM 358 at Kings Park, in nests of an unidentified species of the *Iridomyrmex rufiger* group and in nests of *Rhytidoponera violacea* (Forel) at Cooljarloo, as well as in nests of *Melophorus* sp. JDM 358 at Wireless Hill Park. Ants mainly collected potentially viable seeds. Large numbers of black, potentially viable seeds lay discarded in colony middens at all study sites. The numbers of black seeds found around and inside ant nests ranged from 4 (Kings Park) to 49 (Cooljarloo) in 1990. (Kings Park: number of nests = 26, average number of seeds (mean ± SE) n = 4.3 ± 1.2; Wireless Hill Park: 14 nests, n = 9.9 ± 6.9; Cooljarloo: 16 nests, n = 48.6 ± 8.4) Of all seeds found, none had the aril still attached. In all three study sites, between 2 and 5% of the seeds were brown. Although plants produce many more brown seeds than black seeds (see Schatral & Fox in press), brown seeds were collected only infrequently.

Lipid content of seed and aril

The most abundant fatty acids, in both seed and aril are oleic acid, linoleic acid, palmitic acid and stearic acid (Table 2). Qualitative differences in the lipid content between seed and aril were not found. One saturated acid, lauric acid (C12:0), the unsaturated fatty acids C16:1(n-7), C16:1 (palmitic acid) and C18:1 (oleic acid) are relatively more abundant in the food body. C18:2 (linoleic acid) is more common in the seed than in the aril.

Table 2

The abundance of fatty acids in seed and aril of *H. hypericoides* (black seeds only). Abundance is expressed as total % and as a ratio to oleic acid.

Fatty acid	Name	SEED %	SEED Ratio	ARIL %	ARIL Ratio
12:0	Lauric	low*	-	0.4	0.8
14.0	Myristic	1.3	3.5	0.7	1.4
16:0	Palmitic	19.8	53.5	26.8	45.9
16:1		2.1	5.8	2	4.3
16:1 (n-7)	Palmitic	0.3	0.9	4.6	9.8
17.0		low*	-	0.31	0.7
18:0	Stearic	8.4	22.7	6.2	13.3
18:1 (n-9)	Oleic	37	100	46.7	100
18:1		0.6	1.7	0	0
18:2 (n-6)	Linoleic	28.4	77	11.0	23.6
18:3 (n-3)	Linolenic	0.6	1.5	0.3	0.7
20:0	Arachioic	0.5	1.5	0.5	1.2

* The amount was too small to be measured accurately.

collected than black seeds with arils. Thus, 80 % of the black seeds with arils were taken back inside nests but only 53.3 and 46.7 % of the brown and black seeds without arils, respectively, were taken. Brown seeds as well as black seeds without arils are attended for significantly shorter time periods (analysis of variance, $F_{2,42} = 5.53$, $p<0.05$) than seeds with arils (time attended: n = 15; black seeds with aril, 40.4 ± 5.8 min; black seeds without aril, 13.9 ± 2.6 min; brown seeds, 15 ± 2.5 min). After the seeds had been introduced, ants took only a few minutes to detect them. Seeds were usually attended by 2-12 minor morphs simultaneously (ants of the genus *Melophorus* show continuous polymorphism, J Majer, *pers. comm.*). However, in most cases a major morph helped to carry the seeds inside the nest. The time that elapsed until the ants carried the seeds back to the nest was not significantly different (analysis of variance, $F_{2,21} = 0.014$, NS) for black seeds enclosed by an aril and brown and black seeds without arils respectively (time taken to carry seed to nest: black seeds with aril, n = 11, 34.1 ± 6.3 min; black seeds

without aril, n = 7, 34.7 ± 6.5 min; brown seeds, n = 6, 35.7 ± 5.7 min).

Ant dispersal and its effect on seed germination

Seed germination is similar in sand collected around ant nests and sand collected elsewhere in the same habitat. During the first season, seeds germinated significantly slower (analysis of variance, $F_{3,15} = 4.28$, $p<0.05$) in sterile river sand than in any of the three natural soil treatments (Table 3). However, the number of germinating seeds was not different between soil treatments after half of the experimental time period had elapsed and at the end of the experiment (analysis of variance on arcsine transformed data, after 50 % of time; $F_{3,15} = 1.1$, NS; at the end of the experiment; $F_{3,15} = 0.11$, NS). During the second season, seeds started to germinate significantly later in river sand than in any of the natural soil treatments ($F_{3,11} = 14.4$, $p<0.05$). After half of the experimental time had elapsed, none of the seeds had germinated in river sand but a small percentage of the seeds in the natural soil treatments had done so (Table 3). The number of germinating seeds was not significantly different between the natural soil treatments ($F_{3,8} = 17.11$, $p<0.05$). At the end of the experiment, the final germination percentage was similar for river sand and the three natural soil treatments ($F_{3,8} = 0.009$, NS).

Table 3

Germination of seeds of *H. hypericoides* (mean ± SE, %) from 4 soils over two seasons: First day of germination (mean ± SE), germination (mean ± SE, %) after half of the experimental time period had elapsed and at the end of the experiment. n = number of replicates (= sand trays, 25 seeds per tray). During the second season, fewer replicates were available since no germination was recorded for several trays.

First Season 1991		First day of Germination	Germination %	
			After half of the experiment	At the end of experiment
Soil Type	n			
random	5	59 ± 6.2	10.0 ± 4.0	11.2 ± 4.3
bushes	3	76 ± 8.5	5.3 ± 2.7	9.3 ± 5.8
ant nests	5	54 ± 9.3	6.0 ± 2.0	6.4 ± 4.9
river sand	6	108 ± 15.0	4.3 ± 4.3	9.3 ± 4.9

Second Season 1992		First day of Germination	Germination %	
			After half of the experiment	At the end of experiment
Soil Type	n			
random	4	76 ± 4.8	4.5 ± 1.5	5.5 ± 1.5
bushes	3	65 ± 2.9	4.5 ± 0.9	5.0 ± 0.6
ant nests	4	74 ± 4.1	3.0 ± 0.6	4.5 ± 0.9
river sand	4	123 ± 10.6	0	6.0 ± 2.3

Survival of seedlings in the field

Seedlings were found close to, or on, seven of 40 (17.5 %) ant nests at Wireless Hill Park and Kings Park in December 1991. The number of seedlings ranged from 2 to 15 (mean ± SE, 5.4 ± 1.67). Seedlings were also observed underneath parent plants, but the average number of germinating seeds was lower; of 60 plants examined, seedlings were detected underneath 19, with the average number of seedlings of 1.3 ± 0.13. By June 1992, none of the seedlings had survived, regardless of its germination site.

DISCUSSION

Melophorus sp.1 (ANIC) is one of the most significant seed takers in the northern jarrah forest (Majer 1982). These ants collect elaiosomes although they sometimes consume entire seeds, depending on seed size (Majer 1982). However, the species is omnivorous, with arthropod fragments and seeds found scattered around the nests. Other *Melophorus* species are considered granivores (Davidson & Morton 1981a). Details of the ecology of *Melophorus* sp. JDM 358, the most significant collector of *H. hypericoides* seeds in Kings Park, are unknown. At Cooljarloo, *Rhytidoponera violacea* and *Iridomyrmex rufoniger* sp. collect seeds of *H. hypericoides*. In contrast, species of the genus *Iridomyrmex* have never been recorded eating seeds.

Seeds of *H. hypericoides* drop passively to the ground as soon as they are ripe (dispersal mechanism is of the *Viola odorata* type; Sernander 1906; Berg 1975; Drake 1981). Once dropped from the plant onto the ground, the seeds are removed rapidly. Similarly, ants in the dry sclerophyll forest on North Stradbroke Island in Queensland remove virtually all elaiosome bearing seeds within two days of seed fall (Drake 1981). The high removal rate of *H. hypericoides* seeds suggests that only few seeds remain underneath the parent plant, and therefore most seedlings would escape competition with the parent plant and possible predators underneath the plant. However, the accumulation of seeds around ant nests may cause strong competition with siblings (see below). It is not known whether seeds of *H. hypericoides*, once collected by elaiosome-consuming ants, are subsequently removed by seed-feeding animals (see Hughes & Westoby 1992b for a discussion of this problem).

Since *Melophorus* sp. JDM 358 removes black seeds of *H. hypericoides* still enclosed by an elaiosome in preference to brown seeds and black seeds without the elaiosome, they must be able to discriminate between these seed types. Ants appear to choose between different seeds on the basis of size and/or the chemical compositon of the elaiosome. It has been found that the presence of elaiosomes increases the removal rates by *Rhytidoponera metallica* (Hughes & Westoby 1992b) and other ants (Majer 1982; Oostermeijer 1989; Drake 1981; Hughes & Westoby 1992b). Moreover, ants can distinguish fertile *Eucalyptus regnans* seeds from chaff, and a reducing, sugary substance is regarded as the attractant (Ashton 1979).

The chemical analysis demonstrates that both the aril and seed of *H. hypericoides* are rich in the same fatty acids. The elaiosomes of many plants are rich in lipids, but the composition of the lipids varies between species. Oleic acid is the major fatty acid present in the elaiosomes of *Hepatica americana*, *Viola odorata* and four other ant-dispersed North American herbaceous plants (Marshall *et al.* 1979, Skidmore & Heithaus 1988; Kusmenoglu *et al.* 1989). Oleic acid is also abundant in both elaiosome and seed of *H. hypericoides*. Oleic acid and especially 1,2 diolein, a diglyceride which is derived from oleic acid, are the main attractants for seed

collecting ants (Marshall *et al.* 1979; Skidmore & Heithaus 1988; Brew *et al.* 1989; Kusmenoglu *et al.* 1989; Hughes & Westoby 1992b). In contrast, Bresinsky (1963) suggested that the diglyceride ricinolic acid attracts ants to the elaiosomes of *Viola odorata*. Further studies are necessary to determine which chemical substance in the elaiosome of *H. hypericoides* induces seed carrying behaviour in ants.

Germination of *H. hypericoides* seeds in sand collected from ant nests is not enhanced compared with germination attained from sand collected underneath bushes, randomly collected sand and river sand. However, the conditions inside an ant nest will be more complex than the experimental conditions. Moisture, temperature, aeration and the presence of microorganisms may affect the germination of seeds in nature. Since seeds germinated more slowly in sterile river sand than in the natural soil treatments, river sand may lack nutrients and/or certain micro-organisms that promote the successful germination of seeds in natural soil.

The death rate of seedlings observed in the field may be increased as a result of competition on the ant mounds (Beattie & Lyons 1975; Shea *et al.* 1979), although this hypothesis does not explain the equally high death rate for seedlings that grow underneath parent plants. Competition between siblings would be mainly for nutrients and water. The nutrient content of the soil has not been analysed during the present study on *H. hypericoides*. Majer (1982) has found no differences in total nitrogen or available phosphorus contents between soils from *Melophorus* sp. 1 (ANIC) nests and soils from control areas 1 m away from each nest. In contrast, nutrients are concentrated locally on the mounds of some other ants (Davidson & Morton 1981b). Drake (1981) is sceptical of the hypothesis that ant nests are beneficial germination sites. It is not only that seed dumps may cause high competition between seedlings, but the nests of some myrmecochorous ant species do not appear to offer suitable germination conditions. Nests of *R. metallica*, for instance, are sometimes located in tree trunks and germination is highly unlikely because of the restricted depth of soil available.

Whether the removal of the aril benefits seed germination is unknown for *H. hypericoides* but it promotes germination in *H. cuneiformis* (unpublished data). Similarly, Horvitz (1981) found that the germination of the tropical perennial herb *Calathea microcephala* was enhanced by the removal of the elaiosome.

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**PLANT DISEASES IN
ECOSYSTEMS: threats
and impacts in
south-western Australia**

Locality map of main towns and features mentioned in the volume.

Locality map of main towns and features mentioned in the volume.

Southwestern Australia

Indian Ocean

250 km

N

- Eneabba
- Cervantes
- Moore River
- Gingin
- Bullsbrook
- Perth
- Karragullen
- Garden Island
- Cardup
- Popanyinning
- Yalgorup
- Dwellingup
- Cape Naturaliste
- East Mount Barren
- Hopetoun
- Esperance
- Dunsborough
- Kojonup
- STIRLING RANGE
- Fitzgerald River
- Augusta
- Bremer Bay
- Cape Le Grand
- Cape Arid
- Cape Leeuwin
- Kamballup
- Cape Riche
- Walpole
- Cheyne Beach
- Point D' Éntrecasteaux
- Two Peoples Bay
- West Cape Howe
- Albany

150 km

Wills 94

Front Cover artwork: honey possum (*Tarsipes rostratus*) on a nodding Banksia bloom (*Banksia nutans*) from south coast heathlands threatened by dieback; photograph provided by Steve Hopper, Kings Park and Botanic Gardens, Perth.

Plant Diseases in Ecosystems:
Threats and impacts in south-western Australia

Edited by

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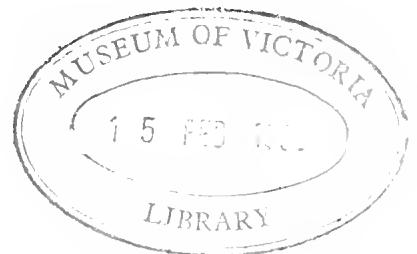
HONORARY EDITOR'S PREFACE

This symposium, on *Plant Diseases in Ecosystems: Threats and Impacts in South-Western Australia*, was jointly organised by the Royal Society of Western Australia and the Ecological Society of Australia, and was sponsored by the Australian Nature Conservation Agency, Alcoa Ltd of Australia, and the Gordon Reid Foundation for Conservation. Its purpose was to bring together a multidisciplinary group of researchers studying various aspects of the ecological, economic and social impact of plant diseases, including *Phytophthora, Armillaria* and canker, in the natural ecosystems of south-western Australia.

This volume presents a summary of the symposium, session summaries, and papers reflecting the presentations of invited speakers in the sessions. These papers have been peer-reviewed, and the editors of this volume are grateful to the following reviewers for their efforts in ensuring that a high scientific standard has been maintained, and for their prompt cooperation:

> M Brown (Forestry Commission of Tasmania, Hobart)
> E Davison (CALM, Manjimup)
> B Dell (Curtin University, Perth)
> D M Cahill (Australian National University, Canberra)
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> K Old (CSIRO, Canberra)
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> R Shivas (W A Department of Agriculture, Perth)
> J A Simpson (State Forests of NSW, West Pennant Hills)
> K Sivasithamparam (University of Western Australia, Perth)
> M Sweetingham (WA Department of Agriculture, Perth)
> G Weste (University of Melbourne, Parkville)
> R T Wills (WA Herbarium, CALM, Perth)
> R Wooller (Murdoch University, Perth)

Abstracts of the invited papers and contributed posters, as well as a list of symposium registrants, are presented elsewhere, in *The Handbook of the Symposium on Plant Diseases in Ecosystems: Threats and Impacts in South-Western Australia*, which is available from the Royal Society of Western Australia for $A10 including postage.

<div align="right">

P C Withers
Honorary Editor
Royal Society of Western Australia

</div>

Foreword

Phytophthora cinnamomi is regarded as one of the most devastating pathogens in natural ecosystems yet recorded. Across southern Australia, it has had a major impact on a wide range of plant species from small shrubs to large eucalypt trees, the most notable of which are the majestic jarrah trees (*Eucalyptus marginata*) of south-western Australia. Little is known about when or how the fungus established itself in south-western Australia, but few doubt the fact that it was introduced by European settlers. Considerable effort has been expended in researching the biology of *P. cinnamomi* and the disease it causes, but are we any closer in answering key questions? Why is the disease spreading so rapidly today in reserves and parks on the south coast, such as the Stirling Ranges? What is the impact of radical ecological changes, such as clear-felling or prescribed burning of forests, on dieback and other diseases? What environmental conditions are conducive to dieback development? Many such questions will be explored in this Volume, sometimes challenging conventional views about ecosystem management for disease control.

P. cinnamomi is not the only pathogen causing widespread destruction of natural ecosystems in south-western Australia. Several canker fungi have been reported causing severe dieback in coastal shrublands and Banksia woodlands, sometimes following the tracks left by a single vehicle several years earlier. What changes are occurring in these ecosystems that may be enhancing disease development? How can society resolve the conflict that occurs between those that want access to these ecosystems for economic or recreational reasons, and the need to control spread of disease?

The Royal Society of Western Australia is in a unique position, as a multi-disciplinary scientific society, to bring together scientists from a wide range of disciplines to discuss issues of importance in a Symposium setting. However, plant diseases in south-western Australia have such a wide-reaching impact on ecosystems, including plant, microbe and animal life, that the *Plant Diseases in Ecosystems Symposium* would not have been possible without the full backing of the Ecological Society of Australia. The only major research done on the impact of plant disease on mammal populations is in eastern Australia. The Ecological Society of Australia brought key scientists to the Symposium from across Australia, and helped to involve the Australian Nature Conservation Agency (ANCA), which funds dieback research at the national level. ANCA fully supported the Symposium with the opening address from its Director, and in generous sponsorship of this publication.

This document is a valuable summary of current and past research into plant diseases in ecosystems that is relevant to the whole of southern Australia. It is one of the few (if not the only) compilations on the subject, and is of course a major reason for holding the Symposium. The Symposium allowed a wide range of views to be aired, and not all views are supported by data. In many cases, data is simply not available. This has lead to conflict in the past among researchers, and such conflict can only be resolved by identifying the problems and setting about solving them. This Symposium has, we hope, allowed many participants to define the important issues, or to see old issues from new perspectives. One such issue is the effect of environment on development of dieback in jarrah. It is clearly very important to identify the key environmental parameters for disease development so that management strategies may be aimed at reducing disease impact.

Private industry is keenly aware of its responsibilities in its management of native ecosystems, and industry representatives presented papers at the Symposium. We are grateful for support received from industry for the Symposium, and we thank Alcoa of Australia Ltd for their generous sponsorship of this publication.

As organizers of the Symposium, we have attempted to provide a fair and balanced treatment of the subject by inviting a wide range of participants from all institutions that are actively involved in research into plant diseases in ecosystems, with an emphasis on south-western Australia. One resounding conclusion from the Symposium was that more research is needed into the effect of diseases on ecosystems, and that management decisions must be based on sound knowledge from research. We believe that a measure of success of the Symposium will be closer interaction among scientists and administrators in the future to achieve this result. This document should help both groups to plan and execute good research.

We would like to thank all those who volunteered their services to help run the Symposium. We thank the Gordon Reid Foundation for financial assistance with running costs and to allow us to publish a Handbook of Abstracts on the day of the Symposium. Last, but not least, we thank our families who endured another bout of late nights and long days.

W A Cowling
President, 1993/1994
Royal Society of Western Australia

and

R T Wills
Honorary Bulletin Editor
Ecological Society of Australia

Plant Diseases in Ecosystems: threats and impacts in south-western Australia

Symposium Summary

S H James

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This symposium reflected the levels of awareness, competence and action focussed upon the problems of plant diseases in Western Australian ecosystems. The problem of *Phytophthora cinnamomi*, the major pathogen in our plant communities, has been likened to a massive invasion[2]. While it is unlikely that the invader will ever be routed, this symposium may help in formulating appropriate strategic and tactical responses to impede its progress and minimise its destructive effects.

Peter Bridgewater[1] outlined the Commonwealth Government's legislative interest in and financial support of dieback research. He emphasised that disease in plant ecosystems was a problem affecting a large proportion of the Australian continent and that the diseases were permanently altering ecosystems, eliminating many keystone species and leaving behind a considerably less diverse community of resistant survivors. In the south-west land division of Western Australia some 1500 to 2000 of the approximately 9000 extant species were susceptible to *P. cinnamomi*, the major pathogen causing dieback disease, but a number of additional pathogens were involved. The reason why such a large proportion of the native flora was susceptible to dieback diseases was a question still not properly answered. The point was made that research and management practices should beware of concentrating upon the curing of symptoms rather than attacking the disease. This puts in sharp focus the possibility that plant diseases in ecosystems may well be a symptom of a more deeply seated ecological malaise. The basic malaise is obviously human involvement in ecosystem dynamics, both direct and indirect, and the minimisation and rectification of the damage resulting from plant diseases in natural ecosystems must clearly involve land management procedures.

Frank Podger[2] likens the advance of *P. cinnamomi* in our plant communities to an invasion and considers it essentially unstoppable so that it will ultimately infect and affect all the available population systems within the continent. He attributes the entry and the primary spread of the disease directly and unequivocally to the activity of man, but is optimistic about our ability to slow its progress.

Bryan Shearer[3] outlined the taxonomic constitution, distribution and impact of four classes of disease producing fungal pathogens in native plant communities in south-western Australia. As well as *Phytophthora*, of which *P. cinnamomi* is the most destructive, *Armillaria leutobubalina* is a very important rootrot fungus which possibly has a wider host range than *Phytophthora*. There is a variety of stem canker fungi and rusts. *Armillaria*, the stem cankers and rusts are probably endemic fungi normally with restricted impacts, but are they becoming increasingly important as hitherto undefined ecological balances become perturbed. Expanded taxonomic research and an inventory of disease incidence is required to document the importance of these pathogens, as well as that due to *Phytophthora*.

Elaine Davison[4] provided evidence strongly suggesting that dieback symptoms and death may be induced in jarrah as a consequence of waterlogging, even without *P. cinnamomi* infection. However, the waterlogged conditions may promote pathogen activity, and secondarily result in increased levels of infection. This is indeed a situation where symptoms and disease may be easily confused.

Ray Wills and Greg Keighery[5] reported that 38% of 460 plant taxa examined are susceptible to *P. cinnamomi*, while 59% of 436 taxa were sensitive to canker fungi. Some 86% of Proteaceae species are susceptible to these pathogens, and after infection the percentage cover of dominant Proteaceous species may be reduced by 95%. The species removed are often keystone species, providing food, cover and nesting resources for associated animals[7] and altering the light regimes necessary to support erstwhile associated plants. Removal of the dominant species by *P. cinnamomi* and canker disease leaves a simpler, less diverse community dominated by rushes and sedges. While these remnants are resistance to *P. cinnamomi* and canker diseases, they are susceptible to a suite of smuts and rootrots[6], and the subsequent performance of these residual populations is conjectural.

While the effect of plant diseases in the loss of diversity and structure of complex plant communities is quite striking, it may not be recognised as such by an untrained observer. Nick Malajczuk and Martin Pearce[8] emphasised that the changes induced in the soil microflora and microfauna may be equally or even more dramatic. He pointed out that the taxonomic complexity of the soil microorganisms is orders of magnitude greater than that of the above ground

vascular plants, and that some 50% of the energy captured by plant photosynthesis finds its way into maintaining the rhizosphere. We are only beginning to chart the dynamics of rhizosphere ecology.

Stuart Crombie outlined the difficulties in assessing the effects of plant disease on timber production in local forests[9]. The Western Australian forests currently produce some 2 x 10^{6} m[3] timber per annum, from which the state receives about $100 million. In addition, the forests have value in water catchment, tourism and education. The effects of timber harvesting on the spread of disease, however, is pronounced, with the major outbreaks of *P. cinnamomi* being closely associated with logging activities, especially the establishment of road networks throughout the forests[2]. Much of the expense associated with timber harvesting is presently concerned with the implementation of disease minimisation.

Ian Colquhoun and Anthony Petersen outlined the dieback control and environmental restoration measures adopted by Alcoa of Australia and RGC Mineral Sands Ltd[11]. Dieback control is a source of additional costs in both industries, but probably represent less than 0.5% of the value of the industries per year.

Industries dependent upon the products of natural plant communities and the threats posed by plant diseases were outlined by Chris Robinson and Ray Wills[10]. Minor industries include honey production ($2 million *per annum*) and cut flowers ($18 million *per annum*). Both these industries are severely affected by plant diseases, but both may ultimately become based on cultivated native plant farms. The tourism industry in Western Australia is a major source of wealth, ($3 billion *per annum*), but only an indeterminate fraction of this industry can be attributed to the attraction of our native plant communities and it is not clear that any changes wrought by plant diseases have diminished that attraction.

Kelly Gillen and Anna Napier[12] reviewed the management of access for recreational activities in the control of dieback diseases in native plant communities. Public access is clearly critical in the spread of dieback. The severe impact of *P. cinnamomi* on almost 75% of the Stirling Range National Park demonstrates the effect of facilitating recreational use in spreading disease. Management of access requires considerable resources in planning and providing appropriate surfaces and drainage patterns, the implementation of seasonal or permanent closure, and the provision of washdown facilities.

Giles Hardy *et al.* reviewed a wide variety of techniques now available for the detection and control of plant pathogens in native plant communities[13], and Jen McComb *et al.* showed that the breeding and cloning of native plants resistant to some pathogens is possible[14]. However, the costs of implementing these "solutions", the large number of imperilled species and the extensive area of infection necessitates a system of prioritisation. Some targeted species and some targeted communities may be protectable at substantial costs.

Greg Keighery *et al.* showed that almost every human activity in and near native plant communities is likely to create an ecological imbalance and to promote the spread of disease[15]. Ecosystem changes wrought by the diseases, especially in association with land clearing and a new set of grazers, predators, pollinators and weed competitors, is permanent. Joanna Young suggested that disease spread and the threat to our flora and its associated fauna may be reduced by land management practices which take basic ecological principles into account[16]. It is, however, arguable that many of the pertinent ecological principles are not yet known or are inimical to our society's requirements.

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[2] History of Research: F D Podger

[3] Major plant pathogens in ecosystems: B L Shearer

[4] Role of environment in dieback of jarrah: E Davison

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[10] Threats of plant disease to flora-based industries: C J Robinson & R T Wills

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[12] Management of access: K Gillen & A Napier

[13] Control options of plant pathogens in native plant communities in south-western Australia: G E St J Hardy, P A O'Brien & B L Shearer

[14] Future ecosystems - use of genetic resistance: J A McComb, M Stukely & I Bennett

[15] Future ecosystems - ecological balance: G J Keighery, N Gibson & D J Coates

[16] Future ecosystems - effects of plant disease on Society: J T Young

Session 1: Biology

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The first paper scheduled for this session was a personal account of the impact of European settlement on native vegetation communities as seen from the perspective of a plant pathologist, and focussing on *Phytophthora*-induced dieback. The paper was presented by Dr Frank Podger and was based on his career-long involvement in the study of diseases of forests and native plant communities, including the first association of *P. cinnamomi* with jarrah dieback. He pointed out that *Phytophthora*-induced diseases of native vegetation is a national problem, with regional circumstances of climate, soil and vegetation differences demanding differing approaches to management. Accidental introduction of *P. cinnamomi* into native vegetation has caused major changes in plant communities and despite the enhanced level of awareness of the consequences of disease, there are major difficulties in achieving containment. He pointed out the dangers of over-emphasis on reductionist research which may provide information that cannot be translated to practical solutions for reducing the spread and impact of *Phytophthora* spp. and advocated a holistic approach to disease management.

Although it was appropriate for a paper on *Phytophthora* to lead this session, the second speaker, Dr Bryan Shearer, gave a much broader picture of the range of pathogens that currently affect the health of native plant communities in south western Australia. He pointed out the need for systematic disease surveys of such communities, and the need to maintain adequate mycological expertise within government agencies and the universities. Without such skills, the recognition and containment or control of epidemics will not even be attempted. A database, which is being compiled for a wide range of families and their diseases, is a first essential step in an assessment of the significance of the main groups of diseases including root rots, stem cankers and leaf diseases.

The final paper in the session was a discussion by Dr Elaine Davison of the role of environment in the dieback of jarrah, especially the effects of waterlogging on the physiology and anatomy of tree roots, and root infection by *P. cinnamomi*. Although the epidemic disease, which is so damaging on the understorey and ground cover in the jarrah forest, Banksia woodland and heathlands, appears to have a somewhat simple etiology, the impact of the fungus on large jarrah trees is more cryptic. Of the several hypotheses to explain local and rapid death of large trees in the jarrah forest over the last two decades, none have proved to apply unequivocally to all circumstances. This partly reflects the inherent difficulty of diagnosis of dieback diseases in large trees. However, controlled glasshouse studies coupled with field investigation suggest that periodic waterlogging may contribute to death by direct effects on root conductivity (through induction of tyloses) and predisposition of roots to infection by *P. cinnamomi*.

The three papers emphasised the need for a multidisciplinary approach to the management of dieback diseases of native vegetation. Systematic gathering of information and rigorous study of the etiology of diseases, host pathogen interactions and of environmental effects are needed for the development of effective management prescriptions.

Session 2: Impact on Ecology

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An ecological perspective on plant diseases in south-western Australian ecosystems is fundamental to appreciating impacts and possible solutions. The inter-relationships and processes linking organisms and their environment are diverse, often complex, and ever changing. The more components there are in ecosystems, the greater the complexity in ecological relationships and processes.

It should come as no surprise, therefore, that in a region of the world with exceptional diversity in its terrestrial vascular flora and marine algae, the ecological impacts of plant diseases are profoundly diverse and subject to no simple solutions. The four papers in this session have admirably illustrated this observation.

The environmental focus of ecology leads us to question what might be special in south-western Australian ecosystems to lead to the plant epidemics we are witnessing today. Factors that deserve consideration include:

- an ancient flat landscape with soils that are predominantly acidic, highly leached and nutrient deficient, and drainage is often sluggish or unco-ordinated (*diseases such as dieback thrive in acidic moist soils*);

- an exceptionally rich vascular flora, that has evolved in isolation for a long time, and with a bewildering array of adaptations to cope with nutrient deficient soils, many involving symbiotic partnerships with microorganisms such as mycorrhizal fungi (*a diverse range of vulnerable hosts for diseases*);

- a modern climatic regime in which districts having the most diverse floras are drought-prone and stressful to plant growth and recruitment (*regular environmental stresses making plants even more vulnerable to disease*);

- a profound, rapid and ongoing human transformation of the landscape following European colonisation, concentrated in farming and industrial districts where the vascular flora is richest *i.e.* the wheatbelt, Swan Coastal Plain *etc* (*human activity places major stresses on native plants through direct destruction or alteration of habitat by fragmentation, altered landscape processes, introduction of weeds and pests etc*).

As eloquently documented by Bryan Shearer, we are faced in south-western Australia with active plant diseases of unprecedented impact and number. Our knowledge of the diseases themselves is rudimentary in most cases. Indeed, there is much more to learn about basic taxonomy and biogeography, let alone ecology, of the majority of the key players in this combination of epidemics. It is estimated, for example, that as much as a third of the 8000+ vascular plants of the south-west of Western Australia have yet to be described, and even higher proportions of the invertebrate fauna and micro-organisms (including the disease agents themselves) are similarly undocumented. Extinction undoubtedly is being played out as we gather our thoughts today.

What can be done? The concept of integrated pest management (Peter Bridgewater, Giles Hardy *et al.*) developed and applied in agriculture, provides a positive model. It requires knowledge of the disease organism, the host and pertinent environmental processes. However, agricultural ecosystems are much simpler in biodiversity than those of concern in south-western Australia, and the economic contribution of agriculture ensures that research is relatively well funded.

A similar model is that of integrated conservation (Falk 1990), but here the focus is on using the full array of *in situ* and *ex situ* approaches to ensure conservation of wild organisms in the face of rapid and potent threats. Tactically, it requires giving priority to those organisms under the greatest threat of extinction (*i.e.* critically endangered taxa). The approach emphasizes the important synergies that arise from an integration and combination of actions taken both in the wild and offsite in botanical gardens or zoos.

Where the situation is critical in the wild, as emphasized by Wills and Keighery for endangered plants, and by Keighery *et al.* for fragmented remnant vegetation infected by disease, the collection and storage of germplasm for future restoration and recovery programs is essential to avert extinction. Fortunately, recent advances in cryostorage potentially offer an economic and long-lasting approach to effective *ex situ* management of the large number of threatened taxa facing extinction in south-western Australia (Touchell & Dixon 1993; Touchell *et al.* 1992).

For the greater majority of taxa and communities under threat, the best way forward would seem to be a combination of containment of the spread of disease, integrated research on the taxonomy, biogeography and biology/ecology of the disease agents, their hosts and associates, and active restoration of communities in areas removed from infection.

Containment is clearly as much a social and political challenge as it is an operational problem. The impact of human activities on wild ecosystems in south-western Australia is pervasive. Part of an integrated approach to disease

management should embrace the best of professional skills in marketing, politics, ethics, education and economics if the public at large is to embrace a commitment to disease hygiene and containment.

Regarding research, it is heartening to see the increasing commitment of funds to the problem from organisations such as the Australian Nature Conservation Agency and Alcoa Australia. The one concern I have is that the need for integrated research is lost sight of — we need to invest our limited research funds wisely, at an appropriate level to understand the disease organisms, their hosts, associated organisms and pertinent environmental factors.

I would hope that allocation of research funds includes targeted support for traditional disciplines such as taxonomy, biogeography, and ecology, as well as modern and currently more popular molecular, genetic and cryobiological approaches, because we need knowledge in all these fields to effectively manage the problem.

The restoration and reconstruction of communities is clearly going to be required as part of the integrated approach to dealing with plant disease. This is a challenging, but potentially most rewarding, field of activity that can capture the imagination of the public at large. The extensive grass-roots support for tree planting in the wheatbelt is a tangible example. A sound knowledge of horticulture is integral to the success of such reconstruction activities, and I see a major role for botanic gardens to play in supporting and working alongside land managers to achieve conservation through restoration ecology.

Symbiosis is an extraordinarily successful strategy among the diverse organisms in ecosystems of south-western Australia. Integrated and collaborative action on our part offers the best chance many of these organisms have for the future.

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Session 3: Impact on Industry

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The assessment of the impact of plant diseases in ecosystems on industries in the south-western part of Australia are varied and depend on the type of organism, the ability of researchers to detect and identify the diseases, and the type of industry. The range of industries impacted by plant diseases include tourism, recreation, conservation, mining, water production, honey production, forestry and flora-based industries (such as medicinal plants and wildflower picking). The papers in this session concentrated on the plant diseases associated with the dieback caused by species of *Phytophthora*, the straw rots caused by *Armillaria luteobubalina*, canker and smut fungi, karri brown wood caused by a variety of fungi and a range of nursery pathogens. While the evidence mostly concerned species of *Phytophthora*, there is a growing awareness of the lack of knowledge on the many plant disease species which may occur in the south-west, which have not been identified or studied. Historically, plant diseases have not been investigated until their effects on the ecosystems have become easily detectable, and usually at this stage the plant disease is well established in the communities concerned. In many cases, the very presence of industry has fostered the research to define the problem and the potential management options for minimizing impacts and costs of these plant diseases

The authors presented a range of data to illustrate the impact of these plant diseases on jarrah production, a range of mining operations, the flora-based industries, and recreational activities. The difficulties faced in determining the type and cost of the impact of plant diseases on the ecosystems are related in part to the underlying site factors (*e.g.* rainfall, geology, soils, topographical positions), the biology of species within the various ecosystems, and the type and location of the various industries. For example, in the case of mining, the operations of Alcoa of Australia and RGC Min-

erals Sands were discussed and despite the very diverse range of site conditions (*e.g.* Darling Ranges and Coastal Plain) there was common recognition of the impact of the species of *Phytophthora* on the operations. In these latter presentations, it was stressed that the impact was more than just financial, although this aspect was still evident from the presentations. Both companies recognise the potential threat of the plant diseases affecting the adjacent natural vegetation, the ability of establishing key plant species in rehabilitation sites, and achieving high species richness in these sites.

The potential impact of all plant diseases on these ecosystems is very difficult to determine as there is lack of taxonomic and basic research on the range of pathogens present in the environment. In fact, the effort of some of the commercial or licensed industries such as forestry and mining have assisted in defining and determining the impacts of the plant diseases in the south-western part of Australia. On the other hand, as Gillen and Napier discussed in their paper, the less controlled or un-licensed activities such as recreation and tourism in some ways pose greater threats to the ecosystems. The wider responsibilities and costs then return to the management authorities, the government departments and ultimately the Australian community to determine equable rules to minimize the spread and intensification of the plant diseases. The latter is achieved primarily through management plans and operational activities (such as closing roads and quarantine measures). The costs associated with these less controlled activities is very difficult to determine as many cannot be determined without a substantial improvement in the understanding of the plant diseases, the ecosystems, the different site conditions and the diversity of activities concerned.

Session 4: The Future

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This session juxtaposed optimism with a sombre realism, if not pessimism. The optimism derives from the promise and achievements of modern technological capabilities and focussed research. The darker view is generated by a global, but rational, view of the magnitude and permeance of the changes in plant communities wrought by dieback diseases and the robustness of the social and economic imperatives which are promoting the spread of those diseases.

Giles Hardy *et al.* presented a broad overview of the current and possible options for the control of plant pathogens in native plant communities. They emphasised the great difference between the vastly diverse natural ecosystems and the monocultures of commercial plant production which provide essentially all our experience in plant disease control, the importance of ecological imbalance in the generation of disease, and the fact that almost every human activity in our native ecosystems promotes imbalance. While phosphorous acid treatment is dramatically effective in mobilising defence responses in certain species otherwise susceptible to *P. cinnamomi*, the general levels of phytotoxicity of this and other chemical controlling measures, and their effects on micro-organisms antagonistic to the pathogen, or otherwise beneficial, are not known. Untargeted chemical application, as per aerial spraying or soil drenching, is potentially capable of inducing deleterious ecosystemic imbalance. Infecting host plants with avirulent or hypovirulent pathogens may increase their resistance to virulent pathogens without any significant perturbation of the ecosystem. It should be possible to construct appropriate hypo-virulent pathogens using ds-RNA elements. Breeding, or selecting, resistant strains of host plants is a demonstrated possibility and there is little doubt that genetically-engineered, resistant hosts will be constructed in the near future. However, the scope for using targeted chemical and biological protectants, and selected or engineered stock is limited because of the cost, the area of bushland infected, and the number of susceptible species involved. Hardy *et al.* also described the sophisticated techniques now available for detecting and accurately identifying pathogens including immunological and DNA based procedures. The paper also reviewed the management procedures which are currently practised, including hazard rating and risk assessment, hygiene practice and quarantine, and outlined the variable expression of *P. cinnamomi*, and other pathogens, with varying ecological conditions.

Jen McComb *et al.* reported a series of studies which show convincingly that resistance of jarrah to *P. cinnamomi* is genetically determined, that their selected resistant stocks are indeed resistant, and that the selected susceptible stocks are indeed susceptible to *P. cinnamomi* when grown in rehabilitated bauxite mine pits. They posed and provided answers to several relevant questions: re-establishment of jarrah in graveyard sites seems possible, but has not yet been accomplished; the technique of selection for resistance and micro propagation could be adapted to any species, but the cost and work involved makes it an option only for selected priority species; the resistant and susceptible stocks available may provide the pedigreed stocks necessary for the detection of molecular markers for *P. cinnamomi* resistance in jarrah; appropriate techniques for introducing genetically engineered resistance into native species in natural ecosystems are presently not in hand and might be subject to public resistance on ethical grounds.

Greg Keighery *et al.* pointed out that the rates of change in Western Australian ecosystems had been dramatically increased since European settlement. Plant disease is but one, albeit extremely important, determinant of ecosystem change, but when associated with the synergism of broadacre land clearing, weeds and arrays of animals utilizing those plants, the change becomes permanent destruction. Rare species which are disease-susceptible and associated with remnant vegetation are fatally threatened. Their remnant ecosystems are often targeted for activities which promote the spread of disease, such as waste disposal and power-line construction. There is likely to be no source for post disease recolonization of remnants in broadacre cleared agricultural areas. A continuing remnantization of native plant communities will promote increasing levels of extinction. Disease within larger continuous areas of native vegetation will promote extinction of susceptible species and domination by fewer resistant species. Stemming this tide of extinction is perhaps the greatest challenge to land management.

Joanna Young emphasised the rapidity and magnitude of change in our plant communities associated with repeated disturbance and human exploitation. Disease may strongly exacerbate these changes, and our experience of disease control in agricultural plant production is not appropriate for disease control in complex natural ecosystems. Young is of the opinion that management must be more strongly aligned with the ecological principles which underly the relative stability of the natural ecosystem rather than being driven by human economic considerations. The natural plant communities and ecosystems of the south-west of Western Australia are diminishing, and will be less available to fewer people in future generations. Our loss can be limited only be management procedures specifically targeted at preservation and protection from disease.

Ecosystem pathogens : A view from the centre (east)

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Introduction

In 1846 to 1851 over a million Irish died, and a million more emigrated, starting a trend which kept the population of Ireland small and the semi-natural ecosystems of Ireland more or less intact, or as intact as a landscape depleted by the British Navy and the Industrial Revolution could be. These deaths and population movements were the result of the Irish Potato Famine, caused by the impact of *Phytophthora infestans* on the Irish potato crop, the introduced potato having become the staple of Irish peasant diet. This syndrome, of an introduced food staple being subject to massive infestation and destruction, is not unknown and may well increase in the next decades as global diversity decreases.

What is interesting, in the context of today's discussions, is that this fungal attack, causing dysfunction to the main Irish agroecosystem, actually saved the Irish landscape, and made it what it is today—one of the best preserved of the European landscapes. The other feature of interest is the candidate of destruction, which is a species of one of the key genera of concern to remaining species-rich Australian ecosystems—*Phytophthora*. Of course, much has now been confused by the misleading use of the term "dieback", being a general phenomenon of arborescent shrubs and trees wherever there are ecosystem stresses. Our focus is on one major, insidious, and relatively unrecognised threat, dieback and die-off caused by fungal attack. Although you will traverse a broader coverage during your discussions today, I want to particularly focus on *Phytophthora cinnamomi*, because it is listed as one of five key threatening processes under the 1992 Federal Endangered Species Act.

Major problem syndromes and areas

In the twentieth century, *Phytophthora* has had a major affect on industries such as nurseries, horticulture, cut flowers, field crops and pastures. In Australia, *Phytophthora* was first recognised as a major problem for flora and fauna with the onset of forest dieback in the jarrah forests of Western Australia and in the mixed eucalypt forests of Eastern Australia.

It has only been more recently, however, that *Phytophthora* has been recognised as having a major impact on Australian biodiversity. In particular *P. cinnamomi* has been identified as causing major ecosystem disruption in the species rich communities of southern Western Australia. In addition cool temperate rainforests, heathlands and the understorey of dry sclerophyll woodlands are affected in Tasmania,

Victoria and New South Wales. In Northern Australia, *Phytophthora* is reported from tropical rainforest, low sclerophyll shrub woodlands, mangroves and heathland. The scale of infestation in South Australia may be only now becoming apparent, with areas such as Kangaroo Island reporting infections.

This insidious pathogen is altering the ecosystems of Australia on a mammoth scale, sometimes in a subtle way, but also dramatically as occurs here in Western Australia. The floristic composition of vegetation communities on a landscape scale are being permanently altered and this is having subsequent impacts on fauna. For example, *Banksia coccinea*, a species highly susceptible to infection by *Phytophthora*, may be a keystone species because of the reliance of birds and small marsupials on its flowers for food.

Relationship with areas of high biodiversity

The effects of *Phytophthora* are most dramatic in areas of high species diversity. In the south-west of Western Australia, for example, it is estimated that 1500 to 2000 species of the estimated 9000 species of vascular plants may be susceptible to infection. Many of these species are highly endemic and have been taken to the edge of extinction. The pathogen is particularly devastating on species from the families of Proteaceae, Papilionaceae, Mimosaceae and Epacridaceae. These families comprise the bulk of species from which the wildflower export and tourism industry relies. For the Proteaceae family, 85% of species found in the Stirling Range National Park have been rated as susceptible to *Phytophthora* (Wills 1993).

Is it possible that areas of high species diversity are more susceptible to *Phytophthora*, or is it simply that it is in these areas that the problem is more apparent because they demonstrate the most stark examples of alterations in community structure? Whatever the answer, the ability of the pathogen to radically reduce the complexity of a community to a relatively fewer number of tolerant species is having a profound affect on the biodiversity of significant regions of Australia.

Many of the species threatened by fungal syndromes in this State, and indeed in the Eastern States, are either poorly known or not yet subject to taxonomic description. It is axiomatic that there are many species becoming greatly diminished, or extinct, without ever being recognised. Now that clearing of land has become recognised as a major problem for biodiversity conservation, it is ironic that the remaining uncleared areas are being threatened by these syndromes. But is it really serious? Is there not so much redundancy (Walker 1992) in these species-rich systems that

the loss of a few, albeit colourful, species will not really be of concern? I pose this as the kind of rhetorical question that will be asked of us by senior bureaucrats and politicians.

Considerations for management at a national level

There are important considerations for a national approach to this pandemic pathogen. These include:

- continuing to develop strategies to control the problem in the short to medium term through effective hygiene, the development of control methods such as the use of phosphonate, and improved prediction and mapping of occurrence of incidence;

- investigating longer term control options that may become available;

- improving communication between agencies and institutions;

- conducting research so that advancements and strategies can be rapidly applied;

- developing a national approach to identifying gaps in knowledge and targeting research towards filling those gaps;

- co-ordinating research that no single agency has the resources or expertise to conduct on its own;

- ensuring that limited resources are well targeted and that the effort is complimentary rather than involving duplication;

- investigating novel approaches to control and management of *Phytophthora* and liaising with international experts and agencies.

Linkage of the problem

The problem of *Phytophthora* has common threads of economic loss and ecosystem breakdown across Australia. However, the relative impact in the various regions of Australia differs. For example, where a complex understorey exists, with associated dependant fauna, ecosystem damage comes from loss of floristic and structural richness leading in turn to loss of faunistic richness. Where death of the overstorey is the most apparent symptom, there can be a resultant change in understorey structure from reduced competition. Climate, geology, soils and the resultant vegetation communities are important factors in determining the relative impact of *Phytophthora* from the north of Australia to Tasmania and the south-west of Western Australia.

The number of researchers involved with *Phytophthora* in natural and agroecosystems around Australia is about 150, which includes research staff, technicians and students. Approximately 75% of the researchers work in Western Australia, Queensland and Victoria. Many horticultural crops, and even subterranean clover, are threatened by *Phytophthora* species. But six species, especially *P. cinnamomi* and *P. megasperma*, are of particular threat to the south coast of Western Australia. In economic terms (wildflowers), the problem could be a loss of upwards of $50 million. But, it is

the incalculable damage to the species rich ecosystems which is of prime concern. How do you measure the change from one of the worlds most species-rich shrublands to a bland covering of grasses, sedges and restioids?

In National Parks and State Forests, quarantine of diseased forest is the main strategy for control in both Western Australia and Victoria. Vehicle check-points and washdown, as well as logging practices which minimise disease spread are other strategies employed. There appears, however, no management practice which is totally successful at eradicating disease originating from infestation by *Phytophthora*.

Given that, research priorities should attempt to focus on Integrated Pest Management (IPM), and yet there seem to be demands from the community for biocontrol or resistance for breeding as the leading research efforts (Cahill 1993). Recent work in Western Australia particularly focuses on the use of phosphorous acid to protect individual trees, and small areas of ecosystems of high conservation value. Other groups have suggested that biocontrol may be feasible, or that hypovirulence could be induced into some populations. Despite these potential developments, the clear message from the current dire situation is that there is no one cure, and that IPM is the only sensible way to go.

Role of the Australian Government

The role of the Australian Government is to promote a national approach and facilitate research and management action. This has been achieved to date through funding and promoting communication between the various parties responsible for research and management.

The Australian Government also has the role of discharging its legislative responsibilities under the *Endangered Species Protection Act 1992* (ESP Act). This new and important legislation tackles endangered species conservation in a number of innovative ways. For example, it provides for the recognition and protection of ecological communities. It also tackles threatening processes, which operate across a range of habitats and affect many species, whether threatened or not. The Act recognises *Phytophthora* as a key threatening process and establishes the premise that a nationally coordinated plan would be of major benefit in tackling the problem. Such a plan must be in place by 1999.

The Commonwealth has significant funding that can be brought to bear on *Phytophthora*, such as from the Endangered Species Program. Important work being funded at present includes the development of disease control by the application of phosphonate, the development of an inexpensive and simple diagnostic test for the presence of *Phytophthora*, the use of GIS for mapping and predicting distribution and severity of disease, and the identification of susceptible taxa and long-term storage of germplasm.

The Commonwealth can also be of assistance by providing research expertise of a high quality to provide direction and support to agencies directly responsible for tackling *Phytophthora*. There are now a number of successful examples of Co-operative Research Centres (CRC) in Australia, where a collaborative and co-operative approach has been employed to tackle important issues such as *Phytophthora*. Given that Integrated Pest Management appears the only

sensible way to tackle the problem, perhaps development of a CRC is a practical and effective way to proceed into an uncertain future. Symposia like this one today are a start on the road to attaining greater certainty.

One final point, which may seem heretical, needs to be posed. Bridgewater & Ivanovici (1992) discuss the phenomenon of "constraint syndromes" on the natural ecosystem, using as exemplars *Drupella* and *Acanthaster* in the marine environment. Are the various fungal syndromes to be discussed today in a similar category? If so, simply solving the problems caused by the fungal species effecting the constraint may not be the whole answer. It would be rather like curing the symptom, rather than the disease. To cure the disease, we suspect a greater understanding is needed of human influences at work in the landscape at large, for broadly-based human-induced change may just be the primary driving forces for the more obvious features such as

dieback/dieoff. Just as IPM may be the answer to solving the fungal problem, we may need to combine it with Integrated Landscape Management, to give full effect to our palliative measures.

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The major plant pathogens occurring in native ecosystems of south-western Australia

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Abstract

Objective assessment of the relative importance of pathogens on conservation and production values in native plant communities of south-western Australia is impeded by the lack of systematic disease surveys. The occurrence of diseases and pathogens on Western Australian native plants was compiled from published information, other reports and personal databases. Pathogens were databased according to name, host name and family, disease group and Botanical Province, giving a total of 936 entries that did not include reports of pathogens on hosts in nurseries. Ninety-one per cent of the pathogen reports were from the South-West Botanical Province and 2% from each of the Eremaean and Northern Botanical Provinces. Bacterial diseases, galls, downy and black mildews, ergot and leaf moulds were infrequently reported on native plants. Pathogens were infrequently reported on species within the families: Aizoaceae, Amaranthaceae, Amaryllidaceae, Annonaceae, Anthericaceae, Apocynaceae, Arecaceae, Asphodelaceae, Cupressaceae, Cyperaceae, Dennstaedtiaceae, Geraniaceae, Juncaceae, Lamiaceae, Linaceae, Loganiaceae, Olacaceae, Onagraceae, Phormiaceae, Pittosporaceae, Podocarpaceae, Polygonaceae, Portulacaceae, Rubiaceae, Solanaceae, Stylidiaceae, Tremandraceae, Verbenaceae and Zamiaceae. Pythiacious root rots, rusts, *Armillaria* root rots, stem cankers, and leaf spots and blights were frequently reported on native plants. Families most affected by disease were: Proteaceae, Myrtaceae, Mimosaceae, Papilionaceae, Haemodoraceae, Goodeniaceae, Epacridaceae, Poaceae and Chenopodiaceae. Families mostly affected by rusts were least affected by the root rots, stem cankers and leaf spots and blights. The biology, distribution and disease expression of *Phytophthora cinnamomi*, rust fungi, *Armillaria luteobubalina* and *Cryptodiaporthe* canker of Proteaceae in native plant communities are described. Conservation of plant taxa requires a much better inventory, than is available at present, of the incidence and status of the various plant pathogens that occur in native communities of south-western Australia. Prediction of the likely long-term effects of pathogens on native plant communities requires a much better understanding of their life cycles and biology in the south-western Australian environment.

Introduction

The lack of systematic disease surveys in native plant communities of south-western Australia impedes objective assessment of the relative importance of the impacts of pathogens on conservation and production values (Shearer & Hill 1989; Shearer 1992a). There have been no coordinated regional surveys of disease occurrence in native communities of south-western Australia, similar to the regular assessment of disease and pest conditions in Canadian forests (Forestry Canada 1993). This is somewhat surprising considering the exceptional species richness and high degree of endemicity of the flora of south-western Australia. At least 7000 species of described native vascular plants occur within the state (Green 1985), of which over 3000 are endemic to the area (Keighery 1992). Knowledge of the diseases of native plant taxa is important for maintenance of long-term conservation and production values, especially in the case of rare and endangered taxa.

Current knowledge of the occurrence, biology and impact of pathogens in Western Australia has mainly accumulated from research initiated in response to potential disease threats to wood production, such as early research on wood rots and jarrah dieback (Shearer 1992b), or from opportunistic individual curiosity and observation. Since the mid 1980's, there has been a growing appreciation of the threat of disease to conservation values (Shearer 1992b).

This paper assesses the relative occurrence of pathogens on native plant species from published information and personal databases and then describes the biology, distribution and disease expression of the major pathogens affecting Western Australian native plant communities.

Diseases and pathogens of Western Australian native plants

Occurrence of diseases and pathogens on Western Australia native plants was compiled from published information and reports (Brandis *et al.* 1984; Brittain 1989; Hill 1990; Shearer 1992a; Shivas 1989; Wills 1993) and from survey and isolation databases of my own and those of S Bellgard, F Bunny and the Plant Health Service, Department Conservation and Land Management. Pathogens were databased

according to name, host name and family, disease group (*e.g.* Pythiacious root rots, *Armillaria* root rots, rust, mildew, *etc*) and Botanical Province. Nomenclature of plant taxa follows that of Green (1985). The database consisted of a total of 936 entries, and did not include reports of pathogens on hosts in nurseries. Because of the lack of comprehensive surveys, the current information is incomplete and the database represents an indication of the occurrence of a pathogen on a particular host species rather than the intrinsic frequency of its occurrence. The number of occurrences within families can give some measure of the pathogens relative importance. The analysis will, however, favour pathogens and plant taxa most studied. The analysis will also favour pathogens with wide host range, and disfavour those with high impact but narrow host range.

Ninety-one per cent of the pathogen reports were from the South-West Botanical Province and 2% from each of the Eremaean and Northern Botanical Provinces. This partly reflects the greater concentration of research activity that has occurred in the South-West Botanical Province.

Disease groups occurring in three or more families and families within which there was three or more occurrences of

a pathogen are shown in Table 1. Bacterial diseases, galls, downy and black mildews, ergot, and leaf moulds were infrequently reported on native plants. Pathogens were infrequently reported on species within the families: Aizoaceae, Amaranthaceae, Amaryllidaceae, Annonaceae, Anthericaceae, Apocynaceae, Arecaceae, Asphodelaceae, Cupressaceae, Cyperaceae, Dennstaedtiaceae, Geraniaceae, Juncaceae, Lamiaceae, Linaceae, Loganiaceae, Olacaceae, Onagraceae, Phormiaceae, Pittosporaceae, Podocarpaceae, Polygonaceae, Portulacaceae, Rubiaceae, Solanaceae, Stylidiaceae, Tremandraceae, Verbenaceae and Zamiaceae. This list of families with infrequent disease does not simply reflect families with few species, as only 25% of the families have 5 or less species and just over a third have more than 40 species (Green 1985). The list may represent families that are relatively disease free, but plant taxa may also be included because of limited investigation of disease occurrence.

Pythiacious root rots, rusts, *Armillaria* root rots, stem cankers, and leaf spots and blights were frequently reported on native plants (Table 1). Families most affected by disease were: Proteaceae, Myrtaceae, Mimosaceae, Papilionaceae, Haemodoraceae, Goodeniaceae, Epacridaceae, Poaceae and

Table 1

Frequency of occurrence of pathogens within disease groups and families for which there was three or more records; less frequently occurring groups and families not included are listed in the text. Totals are for all entries in the database and do not necessarily match the row or column totals.

Family	Pythiacious root rots	Rusts	Armillaria root rot	Stem cankers	Leaf spots and blights	Smuts	Wood rots	Powdery mildews	Crown rot	White rust	Total for all disease groups
Proteaceae	136	3	39	53	27						258
Myrtaceae	55		25	33	17		22	7			161
Mimosaceae	5	73	13		7						98
Papilionaceae	29	7	18		6						61
Haemodoraceae	5	27	1		6				3		42
Goodeniaceae	2	37	1							1	41
Epacridaceae	24		14		1						39
Poaceae		14			1	17					35
Chenopodiaceae		13		4	5						22
Dilleniaceae	12		4		1						17
Asteraceae		11	1					2			15
Rutaceae	7	2	2								11
Colchicaceae		10									10
Orchidaceae		9						1			10
Xanthorrhoeaceae	6		2		1						9
Casuarinaceae	4		3				1				8
Iridaceae	6		1		1						8
Rhamnaceae	1	3	2								6
Apiaceae	1	2	1		1						5
Dasypogonaceae	4		1								5
Euphorbiaceae	2		3								5
Restionaceae			2			3					5
Santalaceae			2		3						5
Sterculiaceae	3	1	1								5
Thymelaeaceae	2		3								5
Ranunculaceae		2	1					1			4
Myoporaceae		1	1								3
Zygophyllaceae		3									3
Total for all families	310	232	147	91	79	25	23	12	4	3	936

Chenopodiaceae. Frequency of occurrence of Pythiacious root rots, *Armillaria* root rots, stem cankers and leaf spots and blights were similar between families, although there was a more frequent occurrence of *Armillaria* root rot in the Mimosaceae than for the other disease groups. In contrast, frequency of occurrence of rusts between families was the inverse of that for the previously mentioned disease groups. Families mostly affected by rusts were least affected by the root rots, stem cankers and leaf spots and blights (Table 1). This is especially the case with the Colchicaceae and Orchidaceae which seem to be little affected by diseases other than rust, although this may also be due to limited research on the diseases of these plant taxa.

Within the most frequently occurring Pythiacious root rots (Table 1), *Phytophthora cinnamomi* Rands accounted for 54% of reports, *P. megasperma* Drechsler for 21% and *P. citricola* Sawada for 13%. Within the rusts, 53% were *Puccinia* sp. and 32% *Uromycladium tepperianum* (Sacc) McAlpine gall rust of *Acacia* species. Only one confirmed *Armillaria* species, *A. luteobubalina* Watling & Kile, is known to cause Armillaria root rot in Western Australia (Kile *et al.* 1983). Of the 17 stem canker pathogens recorded, *Botryosphaeria* sp. was the most frequent (45% of reports) followed by *Zythiostroma* sp. (14%) and *Cryptodiaporthe* sp. (11%). Of the 46 leaf spot and blight pathogens recorded, three species were the most frequently recorded, with each only 6% of reports.

Biology of major pathogens

Knowledge of the life cycle and biology of *P. cinnamomi* in native communities of south-western Australia is derived mainly from research conducted in the northern *Eucalyptus marginata* Donn ex Smith forest (Dell & Malajczuk 1989; Shearer & Tippett 1989), but relatively little specific information is known of the biology of *P. cinnamomi* in non-forest communities. In addition, little specific information is known of the factors affecting spore production, infection and host susceptibility to infection for *Phytophthora* species other than *P. cinnamomi*, rusts, *A. luteobubalina* and stem cankers in the south-western Australian environment.

Phytophthora root rots

Phytophthora spp. are introduced soil-borne pathogens belonging to the class Oomycota, a relative primitive group of fungi having a number of morphological, physiological and biochemical characteristics found in certain protozoa and bacteria and an ancestral affiliation with heterokont algae (Barr 1983). In evolutionary development, *Phytophthora* belongs to a transitional group between entirely aquatic and completely terrestrial fungi. This is reflected in their complex life cycles dependent on moist conditions for survival, sporulation, dispersal and infection, and in the initiation of various adaptation strategies to cope with the fluctuating soil environment.

Phytophthora cinnamomi is a major pathogen in the alternating temperature and moisture mediterranean climate of south-western Australia, despite the fact it is an introduced, moisture-dependent microorganism. This has occurred because movement of infected soil by human activity has spread the pathogen throughout the region (see below). In addition, the soils and topography in conjunction with the

hydrological cycle and susceptible plant communities have provided niches within the soil profile whereby *P. cinnamomi* can survive adverse conditions, and be spread in water or by root-to-root contact to infect the roots of a wide range of hosts. The interactions that have created the diversity of microenvironments and conditions favourable for sporulation, survival, dispersal and infection are detailed in Shearer & Tippett (1989) and can only briefly be described here.

Phytophthora cinnamomi takes advantage of favourable warm and moist soil conditions in autumn and spring, and presence of susceptible tissue, by rapidly producing various spore types in an expanding phase of population growth. During unfavourable conditions of low soil moisture, absence of susceptible tissue, and high microbial activity, the fungal hyphae are lysed and disintegrate, releasing resistant spores specialised for survival. Vegetative reproduction is by sporangia that release infectious motile zoospores in water. This is the main way the *Phytophthora* species reproduce and infect plants. Spherical, sedentary chlamydospores may also be vegetatively produced, but their role in infection and survival in south-western Australia is poorly understood. Under certain conditions, sexual reproduction by thick-walled oospores occurs. Oospore production by *P. cinnamomi* is probably infrequent in south-western Australia as two mating types are required for spore induction but only one mating type predominates in the region. In comparison, *P. citricola* and *P. megasperma* readily produce oospores from the one mating type. Reproduction by oospores is probably an important survival mechanism for *P. citricola* and *P. megasperma* as the thick walled spores are more resistant to drying than are zoospores.

Once *Phytophthora* species have entered the roots of susceptible hosts, primary symptoms of infection are evident as advancing fronts of necrosis (lesions) in the inner bark of roots and stems. Lesions are most evident in fleshy primary roots as a root rot. The fungi kill their hosts by destroying the roots and girdling the base of the stem, depriving the plant of access to nutrients and water. Host plant species occur mainly in the Proteaceae, Myrtaceae, Papilionaceae, Epacridaceae and Dilleniaceae (Table 1).

Rusts

Although rusts are the second most frequent pathogens on native plant taxa in south-western Australia (Table 1), research on their biology in the region is limited to only three studies (Goodwin 1963; Verhoogt & Sivasithamparam 1985; Nichol 1986). Rust fungi are of the order Uredinales of the class Basidiomycota and are destructive pathogens to many agriculture and forest crops. In contrast to *Phytophthora*, rust pathogens on native plants are probably endemic, they complete their life cycles on the above ground plant parts and they are mainly dispersed as air borne spores. Also, unlike root rots and stem cankers which can live and reproduce on dead tissue, the rust fungi are obligatory parasitic, requiring living hosts for normal development.

The life cycles of rusts are more complex than those found in any other group of fungi, and typically consist of four or five reproductive stages in a regular sequence. Details of the stages can be found elsewhere (Agrios 1978) and are briefly described as follows. Pycniospores and receptive hyphae are

produced in pycnia. Pycniospores serve as spermatia and are transferred to other pycnia by insects and fuse to form binucleate hyphae. Aeciospores formed from the binucleate hyphae are wind-dispersed to infect hosts other than the one on which they are produced. Uredospores are produced from binucleate mycelium from a germinating aeciospore or a uredospore. Uredospores are generally the main repeating stage of rusts and can withstand adverse conditions of long-range dispersal from plant to plant by wind. Sexual reproduction is by teleutospores, which are not dispersed but germinate to produce basidiospores. The basidiospores are temperature and moisture sensitive, and dispersed by wind over short distances. Within this life cycle pattern, long-cycled rusts produce at least one type of binucleate spore in addition to the teleutospore, while for short-cycled rusts the teleutospore is the only binucleate spore produced. The life cycle may be completed on the one host (autoecious) or on two distinct hosts (heteroecious).

In Western Australia, gall rust (*Uromycladium tepperianum*) is a short-cycled autoecious rust producing pycniospores, teleutospores and basidiospores mainly on Acacia species (Goodwin 1963). Some rust taxa on orchids are long-cycled as they produce aeciospores, uredospores and teleutospores (Nichol *et al.* 1988). It is not known whether the life cycle of rusts on plant taxa other than the Mimosaceae (Table 1) are autoecious or heteroecious.

Host plant species occur mainly in the Mimosaceae, Goodeniaceae, Haemodoraceae, Poaceae, Chenopodiaceae, Asteraceae, Orchidaceae and Colchicaceae (Table 1). *Uromycladium tepperianum* infection stimulates the *Acacia* host to form galls and/or 'witches brooms' (Goodwin 1963). Infection of the growing point results in a witches broom caused by reduction of the growing axis and a proliferation of lateral buds. Galls may be globose or elongated and can form on different plant organs, although formation on a particular plant part is consistent within an *Acacia* sp. (Goodwin 1963). Gall formation on inflorescences reduces fertilisation and fruit development. Uredospore production by leaf rusts rupture the leaf epidermis, reducing photosynthetic and transpiration processes. In Orchidaceae, leaves infected with rust senesce earlier than healthy leaves and rusted plants produce fewer flowers than healthy plants (Nichol 1986).

Armillaria root rot

Research on *A. luteobubalina* in south-western Australia has mainly concentrated on the impact of the pathogen in forested areas (Pearce *et al.* 1986; Shearer & Tippett 1988; Pearce & Malajczuk 1990a), and the potential for biocontrol with wood decay fungi (Pearce & Malajczuk 1990b). The impact of the pathogen on shrubland and heathland communities has only recently been recognised (Shearer *et al.* 1994). Specific details are lacking on the mechanisms of infection and host colonisation of *A. luteobubalina* in Western Australia and factors affecting host susceptibility to infection (Shearer 1992a). Details of the life cycle of *Armillaria* species are reviewed in Shaw & Kile (1991).

Armillaria luteobubalina is an indigenous species of mushroom-producing primary pathogen of the order Agaricales, class Basidiomycota. Infection from *A. luteobubalina* occurs from aerial dispersed basidiospores or through mycelial transfer at root contacts. Growth through the soil by rhizomorphs is not an important mechanism of spread in south-western Australia (Pearce *et al.* 1986; Shearer & Tippett 1988) as the seasonal pattern of temperature and moisture associated with the mediterranean climate of the region, is not conducive for rhizomorph growth (Pearce & Malajczuk 1990c). Basidiospores, formed by sexual recombination of gametes, are shed in autumn-winter from annual fruiting bodies that develop on decayed roots and stems of dead and living trees. Fruiting bodies of *A. luteobubalina* are mainly produced in June and July (Pearce *et al.* 1986; Shearer & Tippett 1988). How basidiospores infect woody tissue is poorly understood and is probably an infrequent event (Kile 1983). The distribution of infection points and aerial dispersed sexually produced basidiospores results in a discontinuous, discrete distribution of infections of different genotypes. The number and distribution of different genotypes can provide an estimate of the frequency of infection from basidiospores (Kile 1983), but no analysis of this type has been done for south-western Australia. The pathogen spreads within disease centres by mycelial growth through roots. In susceptible *E. wandoo* Blakely, the mean rate of disease extension over a 8 year period was 2.04 ± 1.05 m yr^{-1} (Shearer *unpub. obs.*). This is comparable to mean maximum rates of 0.7-1.6 m yr^{-1} found by Kile (1983) for Victorian forest. New infections are established by contact between roots and stems, and dead roots and stumps increase the inoculum level. In mixed eucalypt forests in the highlands of west-central Victoria, the pathogen can survive in stumps for up to 30 years (Kile 1981).

Armillaria luteobubalina establishes in the bark and causes columns of decay within roots and stems of host species. The pathogen spreads tangentially in the inner bark of susceptible hosts, often resulting in girdling of the stem collar and host death (Pearce *et al.* 1986; Shearer & Tippett 1988). Host plant species occur mainly in the Proteaceae, Myrtaceae, Papilionaceae, Epacridaceae and Mimosaceae (Table 1).

Stem cankers

The contribution of canker fungi to stem and branch death in south-western Australia has largely been ignored (Davison & Tay 1983; Shearer 1992a). Mortality and decline of marri and red flowering gum were associated with stem cankers in the mid 1930's (Smith 1970). Davison & Tay (1983) identified a number of pathogenic fungi associated with stem and branch cankers of forest trees in south-western Australia. In 1989, a species of *Diplodina* (sexual stage *Cryptodiaporthe*) was found killing *Banksia coccinea* R. Brown on the south coast of the state (Shearer & Fairman 1991). Interpretation of the cause of stem cankering can be complicated as some fungi are frequently isolated from cankers but they are secondary invaders of the diseased tissue. *Cytospora eucalypticola* van der Westhuizen is an example of a frequently isolated fungus that pathogenicity tests have shown to be a nonagressive facultative parasite (Davison & Tay 1983; Shearer *et al.* 1987).

The origins of stem canker fungi in south-western Australia are uncertain. *Botryosphaeria ribis* Gossenb. & Dugg. is possibly an introduced pathogen (Davison & Tay 1983) and it is widely distributed on a diverse range of hosts in the tropical and temperate regions of the world. The *Cryptodiaporthe* pathogen of *B. coccinea* is possibly endemic as

it is a new species (Bathgate *et al.* 1994) and has a very limited host range within the Proteaceae (see below).

How the canker-causing fungi complete their life cycles in south-western Australia requires further research. This is complicated by uncertainties in the identity of the various spore stages of canker fungi on native plants in this state. For example, the asexual stage of *Endothia* isolated from Myrtaceae in Western Australia has been identified as *En. gyrosa* (Schw. Fr.) Fr. by isozyme analysis against voucher specimens (Davison & Coates 1991). Even though the sexual ascospore stage occurs in eastern Australia (Walker *et al.* 1985), it has yet to be recorded in Western Australia.

Canker fungi kill the aerial parts of plants. This is in comparison to disease caused by *Phytophthora* and *Armillaria* that kill plants from the roots up. Hosts affected by canker fungi occur mainly in the Proteaceae and Myrtaceae (Table 1). The fungi sporulate in dead bark and are dispersed as sexually produced ascospores in wind currents or asexually produced pycnidiospores in rain splash. The mode of entry of germinating spores is either direct or gained through lenticels or wounds from branch stubs, broken branches and insect damage. Phloem and sapwood invasion results in sunken cracked areas on the stem that may expose the xylem and exude kino. Cankers thus formed can be annual, perennial or diffuse. In annual cankers, lesion development is contained by host defense mechanisms within the first year's invasion. *Botryosphaeria ribis* generally forms annual cankers unless stress factors affect the host-pathogen interaction, as described in the next section. Perennial cankers denoted by concentric rings are formed when invasion by the pathogen is walled off, but the pathogen survives on dead tissue to re-invade healthy tissue in the following years. Large 'target'-like cankers occur on *E. calophylla* Lindley and *E. gomphocephala* DC, but the causal pathogen has yet to be determined. Diffuse cankers occur when lesions rapidly progress along the stem, resulting in gradual decline from death of twigs and lateral branches to rapid death of leaders in a few years. Diffuse canker development by *Cryptodiaporthe* sp. leads to death of infected *B. coccinea*, and destruction of diseased stands in a few years (Shearer & Fairman 1991; see below). The effect of death of canker-infected stems and branches on leaf area and host plant functioning has not been determined.

Disease caused by canker fungi can be aggravated by transient stress factors (Schoeneweiss 1975). Trees planted outside the normal range may experience environmental stress with an associated decline in resistance to infection by canker organisms (Shearer *et al.* 1987). Stress from two days of above 40 °C and high winds in February 1991, was associated with rapid extension of *Bo. ribis* lesions in stems of *B. speciosa* R Brown near Hopetoun. The stand was severely debilitated by the infection and trees died. Twelve months later, many of the surviving *B. speciosa* trees had again contained the *Bo. ribis* lesions and formed new epicormics below the walled-off lesion margin.

Distribution

Phytophthora cinnamomi

Phytophthora cinnamomi is the most common and destructive of the *Phytophthora* species found in native communities of the south-west. It occurs in the area bounded by Eneabba

north of Perth, east of Dryandra near Popanyinning, and Cape Arid east of Esperance on the south coast (Fig 1).
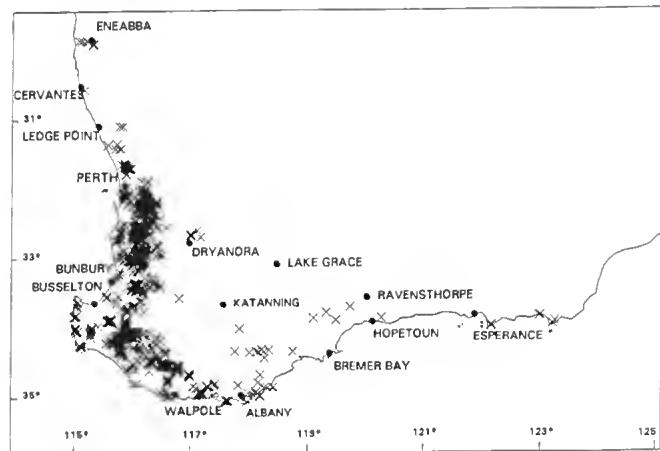
Figure 1. Distribution of *Phytophthora cinnamomi* disease centres in south-western Australia, compiled mainly from assessment plots and mapping, and supplemented by isolation records.

Greatest incidence of *P. cinnamomi* occurs in the northern and southern *E. marginata* forest (Fig 1). This is partly due to environment and partly to historical factors related to human activity (Shearer & Tippett 1989; Shearer 1992a). The pathogen frequently occurs on the acidic leached sands of the Bassendean Dune System of the Swan Coastal Plain, Gavin Sands of the Leeuwin-Naturaliste Ridge, laterite soils and winter wet flats of the d'Entrecasteaux and Walpole-Nornalup National Parks and the Keystone and Gardner geomorphic units in areas on the south coast such as West Cape Howe and Two Peoples Bay. Incidence is high in the sandy deposits of the Stirling Range National Park (the rectangle of occurrences north of Albany, Fig 1). Infections fringe the Fitzgerald River National Park east of Bremer Bay, but a 6 km long infection occurs within the park.

A transect from the coast, inland between 31.5° and 33.5° S, shows that *P. cinnamomi* disease centres are absent from coastal dunes, but increase in frequency in the Bassendean Dune System and Pinjarra Plain to the west of the Darling Scarp (Fig 2). Frequency of occurrence is greatest in the northern *E. marginata* forest on the western edge of the Darling Scarp, decreasing rapidly to the drier eastern edge of the *E. marginata* forest (Fig 2).

Rusts

Rusts are widely distributed on native plant taxa throughout the south-west (Fig 3). This is especially so for *U. tepperianum*, which occurs relatively frequently on *Acacia* spp. in coastal areas and in the eastern wheatbelt and goldfields. *Uromycladium tepperianum* is probably the most widely distributed pathogen in native communities in south-western Australia (compare Fig 3 with Figs 1 and 4-6). However, because of the limited research on rusts of native plants of Western Australia, many more surveys are needed for a more accurate picture of the distribution of rusts in native communities of the state.

Armillaria luteobubalina

Armillaria luteobubalina disease centres mainly occur in coastal dune vegetation and forested areas (Fig 4). In vegeta-
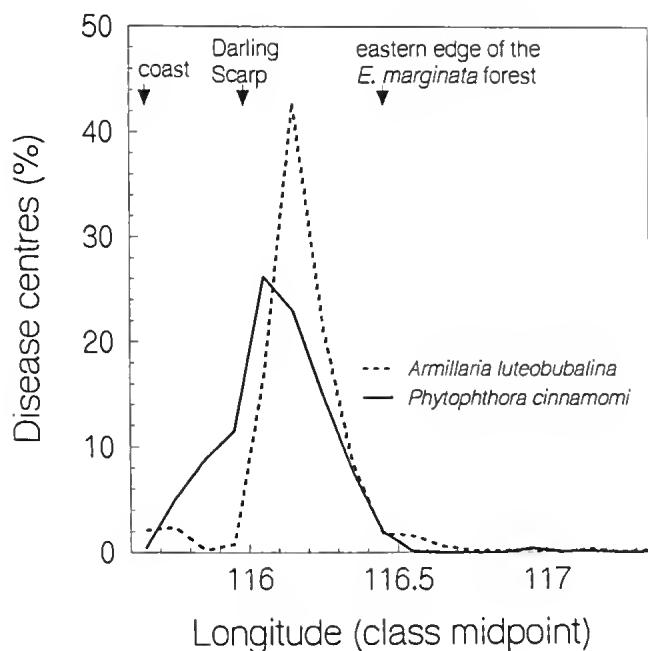
Figure 2. Occurrence of disease centres of *Armillaria luteobubalina* and *Phytophthora cinnamomi* in a transect between 31.5° and 33.5° S and from the coast (115.6° E) inland to 117.4° E. The plot is percentage of occurrence of disease centres in longitude classes of one tenth of a degree.


Figure 3. Distribution of rusts on native plants in south-western Australia, compiled from reports in Shivas (1989) and Nichol(1986). Rust taxa were: *Puccinia* for Haemodoraceae, *Uromycladium* for Mimosaceae, *Aecidium* and *Puccinia* for Asteraceae and Colchicaceae, and *Puccinia* and *Uromyces* for Goodeniaceae and Orchidaceae.

tion on the non-podsol sands of the coastal dunes, *A. luteobubalina* occurs as far north as Cervantes and around the coast to Cape Arid (Fig 4). The pathogen also occurs in *E. gomphocephala* forest and *Banksia* woodland of the Spearwood Dune System and equivalents, just inland from coastal dunes but rarely occurs in communities on the acid sands of the Bassendean Dune System. The pathogen frequently occurs in the northern and southern *E. marginata* forest, the *E. diversicolor* F. Muell. forest in the south, and in *E. wandoo* forest to the east.

Figure 4. Distribution of *Armillaria luteobubalina* disease centres in south-western Australia, compiled from isolation records, assessment plots and mapping.

In comparison to *P. cinnamomi*, *A. luteobubalina* occurs on the coast and rarely occurs in the Bassendean Dune system to the west of the Darling scarp (Fig 2). Distribution within the northern forest tends to be more skewed to the east, than for *P. cinnamomi*, and there is a greater frequency of occurrence in the *E. wandoo* forest east of the *E. marginata* forest (Fig 2).

Stem canker pathogens

Various canker pathogens, mainly on Myrtaceae and Proteaceae, are widely distributed throughout the south-western Australian region (Fig 5). The distribution map is incomplete, however, as there has been inadequate sampling in the eastern wheatbelt and goldfields.

Figure 5. Distribution of stem canker fungi on Proteaceae and Myrtaceae in south-western Australia, compiled from isolation records.

The recently discovered *Cryptodiaporthe* canker of Proteaceae has an interesting discontinuous distribution (Fig 6). On the south coast, the pathogen infects *B. coccinea* throughout its geographic range (Fig 6). However for *B. grandis* Willd. and *Dryandra sessilis* (Knight) Domin, *Cryptodiaporthe* canker only occurs within a small portion of the geographic range of these two hosts. The pathogen has

not been found in an area between the south coast and west coast (Fig 6), even though the area has been sampled (Fig 5). On the west coast, *Cryptodiaporthe* is an aggressive canker of *D. sessilis* north of Perth and on *B. grandis* south of Perth (Fig 6). Curiously, it has been infrequently isolated from these two hosts in other areas, even though these species occur and have been sampled throughout the south-west. Possible causes of this distribution are currently under investigation.
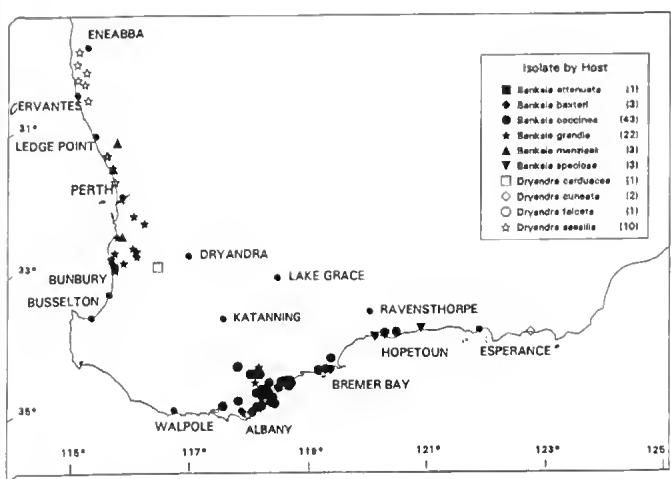
Figure 6. Distribution of *Cryptodiaporthe* stem canker of Proteaceae in south-western Australia, compiled from isolation records.

Communities affected

Phytophthora cinnamomi

Death of the susceptible understorey species of the Proteaceae, Myrtaceae, Papilionaceae and Epacridaceae (Table 1) is the first indication that *P. cinnamomi* has spread into a new area. On sites favourable to disease development, a line of dead and dying understorey marks the 'infection front' at the boundary of infested and uninfested areas (Fig 7). Disease impact is more subtle on less favourable, free draining sites, and there is often no clear demarcation between infested and uninfested areas.

Figure 7. High impact of *Phytophthora cinnamomi* in *Banksia* woodland on the Bassendean Dune System of the Swan Coastal Plain. Most of the overstorey of *Banksia attenuata* R Brown, *B. ilicifolia* R Brown and *B. menziesii* R Brown has died in the infested area. Death of dominant key overstorey and understorey species result in reduction of vegetation biomass in the diseased area and the disease front being delineated by a sharp boundary of dying plants.

Shearer (1990) described the impact of *P. cinnamomi* according to a grouping of vegetation systems of Beard (1981). Impact of *P. cinnamomi* tends to be lowest in coastal communities on coastal limestone and forest communities on relatively fertile red earths associated with major valleys. Impact of *P. cinnamomi* is also low in inland woodlands and shrublands. However, low disease expression in inland areas is probably due to low rainfall unfavourable for pathogen survival and sporulation, rather than a lack of susceptible vegetation or soil profile characteristics favourable for pathogen development (Shearer 1990). This is illustrated by the recently observed infection of rare and endangered *B. cuneata* A S George, located east of Dryandra on the western edge of the wheatbelt (Fig 1).

Impact of *P. cinnamomi* is highest in the *E. marginata* forest understorey on laterites and *Banksia* woodlands associated with leached sands and laterites of the Northern and Southern Sandplains and the Swan Coastal Plain. Within these vulnerable communities, the impact of *P. cinnamomi* results more in changes in community structure and function than in total number of species. For example, infestation of *Banksia* woodland on the Swan Coastal Plain resulted in an average of 7 fewer species in infested than non-infested woodland (Shearer & Dillon 1994). However, the loss of these species often resulted from the almost complete death of the dominant susceptible overstorey and understorey vegetation with a substantial reduction of the vegetation biomass in the diseased area (Shearer & Dillon 1994; Fig 7). Thus in communities dominated by rare and endangered plant taxa, such as *B. brownii* Baxter ex R Brown in the Albany region, infestation is resulting in elimination of the threatened taxa. Keighery (1992) lists 6 species (2 *Andersonia* spp., *B. brownii*, 2 *Dryandra* spp. and *Lambertia orbifolia* C Gardner) that are currently threatened with extinction from *P. cinnamomi* infestation. All of these species of Proteaceae occur in the Southern Sandplains, in areas of high impact of *P. cinnamomi*. Within areas where *P. cinnamomi* has caused significant damage to susceptible communities, such as on the Swan Coastal Plain, the *E. marginata* forest and a number of reserves and national parks on the south coast such as Stirling Range National Park, Cape Arid National Park and Two Peoples Bay Nature Reserve, the main challenge is the development of suitable management strategies for communities irreversibly changed by impact of the pathogen.

Rusts

There is little information available on the impact of rusts in native plant communities of south-western Australia. The impact of rust on native communities of the state cannot accurately be assessed from the current information. Severe infection of *U. tepperianum* ultimately results in death of the host (Goodwin 1963) and the pathogen has been used in biological control of *Acacia saligna* (Labill) H L Wendl, a weed in South Africa (Morris 1991). In Orchidaceae, rust infection reduced the capacity of *Thelymitra crinita* Lindley to produce flowers (Nichol 1986). Thus, rust found on rare and endangered *T. macmillanii* F Muell would need to be considered in conservation plans, as seed production may be reduced by infection (Nichol 1986).

Armillaria luteobubalina

The impact of *A. luteobubalina* disease centres can be expressed as: 1) an expanding patch of dead and dying hosts;

2) dead hosts occurring frequently, but at random, in patches; 3) dead hosts occurring infrequently, but individually, or at random in patches; and 4) small patches of dead and dying hosts occurring in young stands, but the patches of mortality fail to expand as the stand ages. The first and second impact type mainly occur in coastal dune vegetation (Fig 8) and *E. wandoo* forest (Fig 9). The disease centres can be quite large, averaging 1.7 ± 0.2 ha (range 0.02 - 6.5 ha) for coastal dune vegetation (Shearer *et al.* 1994) and 1.2 ± 0.3 ha (range 0.01 - 8 ha) for *E. wandoo* forest (Shearer *unpub. obs.*). Most of the susceptible hosts are killed within the disease centres of coastal dune and *E. wandoo* communities, leaving open denuded areas which encourage severe wind erosion of coastal dunes (Fig 8A). In coastal dunes, geographically restricted *Callitris preisii* Miq (Fig 8B) and rare and endangered *B. brownii* and *B. occidentalis* R Brown *formosa* Hopper are threatened by infection. In the *E. wandoo* forest of the Stirling Range National Park, *A. luteobubalina* infestation is killing *Choretrum glomeratum* R Brown, the only food plant for the larvae of the rare brown azure butterfly (Wills & Kinnear 1993). The third and fourth impact type mainly occur in *E. diversicolor*, *E. gomphocephala* and *E. marginata* forests.

Stem canker pathogens

Stem canker pathogens are having considerable impact in communities dominated by Proteaceae and Myrtaceae in south-western Australia. *Cryptodiaporthe* stem canker is causing high mortality of *B. coccinea* (Fig 10) throughout the Banksia's geographic range on the south coast (Fig 6). In one monitored site, plant death increased from 40% to 98% in 2.7 years. The pathogen is also causing severe branch and stem cankering of *D. sessilis* north of Perth and *B. grandis*, south of Perth. On the south coast, a *Zythiostroma* sp. causes stem cankers of *B. baxteri* and *Bo. ribis* infection has debilitated stands of *B. speciosa* in association with climatic stress.

In eucalypt forest communities, stem canker fungi are associated with crown decline, stem cankering and mortality of *E. ficifolia* F Muell, *E. calophylla* and *E. gomphocephala*. In each case, the causal pathogen has yet to be identified, although *En. gyrosa* and *Bo. ribis* have been isolated from dying *E. gomphocephala* (Shearer *unpub. obs.*). Canker fungi have been associated with the complex of factors causing crown decline in *E. wandoo* (Albone 1989). Cankers are also having an impact on myrtacious dominated communities, other than forest. For example, a *Phomopsis* sp. was isolated from dying branches of *Calothamnus quadrifidus* R Brown showing severe canopy decline throughout the northern sandplain in 1993 (Shearer *unpub. obs.*).

Conclusions

Functional diversity and dynamic balance in native ecosystems result in explosive epidemics of disease being uncommon and limited in space and time (Zadoks & Schein 1979). Why then are such explosive epidemics of *Phytophthora* species, *A. luteobubalina* and *Cryptodiaporthe* canker of Proteaceae currently occurring in plant communities of southwestern Australia? *Phytophthora* species are human introduced pathogens to native plant ecosystems of south-western Australia and their impact is related to the intensity of human activity, occurrence of sub-surface soil moisture and temperature conditions that favour survival, multiplication


Figure 8. High impact of *Armillaria luteobubalina* in coastal dune vegetation. A, Death of dune vegetation in an infested area has resulted in denuded areas subject to wind erosion in Yalgorup National Park; B, Most *Callitris preisii* have died in a disease centre on Garden Island.

Figure 9. High mortality of hosts in an *Armillaria luteobubalina* disease centre in *Eucalyptus wandoo* forest near Kojonup.

and spread of the pathogen and large numbers of susceptible key plant taxa that have not co-evolved with the pathogens. Research has elucidated many of these interactions for *P. cinnamomi* (Shearer & Tippett 1989), but a greater understanding is required for other *Phytophthora* species such as *P. citricola* and *P. megasperma*. In contrast to *Phytophthora*, the situation for *A. luteobubalina* and *Cryptodiaporthe* canker of Proteaceae is different, as they are probably native patho-

Figure 10. A stand of *Banksia coccinea* at Cheyne Beach, east of Albany, killed by *Cryptodiaporthe* canker. Mortality within this stand increased from 40% in 1989 to 98% in 1992.

gens and presumably have co-evolved with the existing vegetation communities. Current knowledge is inadequate to determine whether the prevailing impacts observed relate to a periodic change in disease intensity, or whether they represent more permanent long-term changes.

Conservation of plant taxa requires a much better inventory, than is available at present, of the incidence and status of the various pathogens that occur in native communities of south-western Australia. As noted in this paper, the recording of most pathogen occurrences on native plants in this state is the result of opportunistic research, and comprehensive surveys have yet to be attempted. Pathological research of native plant taxa has tended to be dominated by *P. cinnamomi* to the exclusion of other pathogens. Comprehensive surveys would ensure objective assessment of the importance of hitherto ignored pathogens or pathogen/community interactions. This is illustrated by the recent recognition of the high impact of *A. luteobubalina* in coastal communities (Shearer *et al.* 1994) and *Cryptodiaporthe* canker of Proteaceae (Shearer & Fairman 1991; Bathgate *et al.* 1994). Presumably, these pathogens have been impacting on the respective communities well before their recent recognition. Biogeographical surveys of fauna and flora in communities or National Parks need to include a census of fungi occurring within the areas.

Uncertainties in the taxonomy of fungi in this state complicate inventory of the occurrence and importance of pathogens on native plants (Shearer 1992a). A number of pathogens are undescribed species. This is further complicated by the occurrence of biological species within species complexes, such as may be occurring in *P. megasperma* (Bellgard *et al.* 1994). Fungal taxonomic studies are fundamental to assessment of the relative importance of pathogens.

Prediction of the likely long-term effects of pathogens on native plant communities requires a much better understanding of their life cycles and biology in the south-western Australian environment than is available at present. By their impact, pathogens are undeniably affecting the evolution of plant communities of the state. However there is only a conceptual understanding of the selection pressures pathogens are placing on community composition and functioning, and in turn, the selection pressures environment and community composition are placing on the pathogens. In-

formation on the biology and ecology of pathogens in native communities is needed to determine whether current impacts of endemic pathogens are short term perturbations or part of long term cycles in pathogen-community-environment interactions. Such information is also essential to the determination of the likely consequences of disease, and the application of appropriate control strategies.

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Role of environment in dieback of jarrah:
Effects of waterlogging on jarrah and *Phytophthora cinnamomi*, and infection of jarrah by *P. cinnamomi*.

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Abstract

The association of jarrah deaths with poorly drained dieback sites, following exceptionally heavy rainfall, indicates that hypoxic and anoxic soil conditions, which develop when soil is saturated, may be important in determining why jarrah dies. Experimental work has shown that when jarrah seedlings are waterlogged, xylem vessels in the tap root embolise and are sealed off with tyloses, thus root conductivity is suddenly reduced. Growth and development of *Phytophthora cinnamomi* are also affected because sporulation and vegetative growth are reduced under anaerobic conditions. When jarrah seedlings are inoculated with zoospores, more lesions form on roots in waterlogged soil than on roots maintained in moist soil.

Predictions from these experiments are that in the jarrah forest, soil saturation may directly affect jarrah roots by firstly reducing the number of functional vessels in the sapwood; secondly it will decrease sporulation of *P. cinnamomi* but thirdly will increase the probability of root infection. Less efficient roots and increased infection will affect tree growth and survival.

Introduction

Although 14.2 percent of the jarrah forest is infested by *Phytophthora cinnamomi* (Davison & Shearer 1989), jarrah does not invariably die on all infested (dieback) sites. Groups of trees die suddenly and spectacularly weeks or months after exceptionally heavy rainfall. Groups of jarrah deaths in the late 1940's followed the exceptionally wet winters of 1945-1948 (Harding 1949; Waring 1950), deaths in the late 1950's followed exceptionally heavy summer and winter rainfall in 1955 (Podger *pers. comm.*), deaths in the mid 1960's followed the exceptionally wet winters of 1963-1964 (Podger 1968) and deaths in 1982 followed exceptionally heavy rainfall in January 1982 (Shea *et al.* 1982).

These mass collapse sites, *i.e.* dieback sites where jarrah trees of all sizes and ages die suddenly, are in water gaining situations or are on soils with impeded drainage (Podger *et al.* 1965; Shea *et al.* 1982; Wallace & Hatch 1953; Waring 1950), not on high quality sites with deep, well drained soil profiles (Waring 1950). This association of jarrah deaths with poorly drained sites after periods of excessive rainfall implies that mass collapse occurs on sites in which the soil profile is saturated or partly saturated in the occasional wet years. Thus soil saturation (waterlogging) is an important environmental factor which is associated with jarrah deaths, and which has the potential to affect jarrah, *P. cinnamomi* and root infection.

Symptoms in jarrah and their physiological basis

When jarrah trees die on mass collapse sites, the whole crown turns brown within a few days (Podger *et al.* 1965; Shea *et al.* 1982). These symptoms indicate severe water deficiency which will result if any of the following occur, either singly or in combination: (i) excessive transpiration (*e.g.* following extremely hot weather), (ii) reduced water uptake by fine roots (*e.g.* because the soil has dried out or a large proportion of fine roots have been damaged by pests or pathogens), (iii) reduced conduction of water between fine roots and foliage (*e.g.* caused by mechanical damage or rotting of the sapwood).

Observations of individual jarrah trees prior to crown death shows that there is a rapid decrease in stem girth for several weeks or months before foliage dies (*e.g.* Fig 1; Davison & Tay *unpublished data*). New leaves may still be produced in the crown even though the stem shows symptoms of gradually drying out. The tree shows symptoms of undergoing severe water deficiency which occurs in the stem before the crown, implying that there is either reduced water uptake by fine roots, or there is reduced water movement between roots and foliage.

Water moves between the roots and foliage in sapwood, an outer annulus of lighter coloured wood (xylem). Microscopic examination of sapwood shows that it is largely composed of small, thick-walled cells which give wood its strength and rigidity, and large xylem vessels through which water moves. Xylem vessels are capillary tubes which, in jarrah, are up to 0.4 mm in diameter, and approximately 50 cm long (Davison & Tay *unpublished data*). In sapwood the majority of vessels conduct water, but a few may be non-
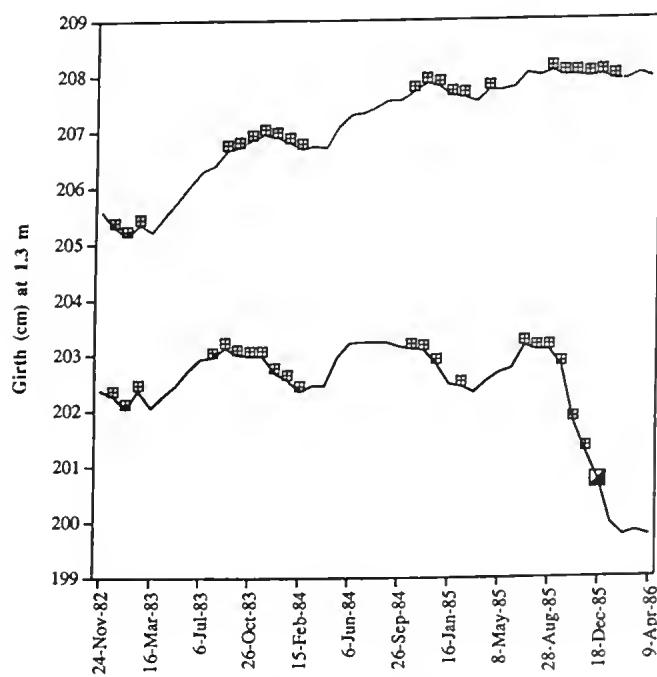
Figure 1. Comparison of girth changes at 1.3 m, leaf production and crown death in two mature jarrah trees of similar girth at Ross Block. One tree was in a dieback site, the other tree was in the adjacent uninfested area. Key: lower trace ——— tree 10, dieback site; upper trace ·········· tree 22, uninfested area; ⊞ young leaves present in the crown; ◣ crown death.

conducting, as indicated by ingrowths, tyloses, from adjacent cells. Tyloses only form in xylem vessels which are gas-filled, not water-filled (Zimmerman 1983). They are one mechanism by which a plant seals off damaged xylem, but it is not known what triggers their formation. Once tyloses form in a xylem vessel, that vessel will never conduct water, so that if there are large numbers of tylosed vessels in sapwood the conductivity will be reduced.

Effects of waterlogging on jarrah, *P. cinnamomi* and root infection

Experimental work

When soil is saturated with water, it becomes anaerobic because oxygen in the soil solution is rapidly consumed by micro-organisms and roots (Drew 1992). As oxygen diffuses 10^4 times more slowly through water than through air, it is used more quickly than it is replaced. Saturated soil will become hypoxic and anoxic more rapidly in summer than in winter, because the solubility of oxygen decreases with increasing temperature, and because respiration increases with increasing temperature. Laboratory measurements using jarrah forest soil show that, when saturated with water, it will become anoxic within 2 days at 20° C, and within 4 to 5 days at 16° C (Davison & Tay 1991). Anaerobic respiration is much less efficient than aerobic respiration so that, quite apart from any other physical and chemical changes in the soil, this sudden development of hypoxic and anoxic conditions is biologically very damaging.

Podger (1967) showed that jarrah was more sensitive to waterlogging than other forest eucalypts. Further work (Davison & Tay 1985) has shown that when jarrah seedlings

are waterlogged under controlled conditions, xylem vessels in the tap root embolise and are sealed off with tyloses, so that roots become less efficient. This happens quickly; the proportion of tylosed vessels is correlated with the duration of waterlogging, and after 14 days at 20° C half of the vessels are blocked. Many woody plants close their stomata when their roots are waterlogged, but jarrah seedlings continue to transpire. Thus, the rate at which seedlings wilt and die depends on both the duration of waterlogging and the transpiration rate of the plants (Davison & Tay 1985).

Waterlogging also affects *P. cinnamomi*, a fungus which requires matric potentials close to zero for the production of sporangia, discharge and dispersal of zoospores (Gisi *et al.* 1980; Shea *et al.* 1983; Kinal *et al.* 1993). Sporulation, however, either does not occur or occurs very slowly under anaerobic conditions (Davison & Tay 1986). Zoospore germination is not affected by aeration, but germ tube growth is correlated with oxygen concentration (Davison & Tay 1986).

Infection of jarrah roots by zoospores of *P. cinnamomi* is greater in saturated soil than in soil at field capacity (Davison & Tay 1987). This is because more lesions are formed as a result of increased mobility of zoospores in flooded soil and increased attraction of zoospores to anaerobically respiring roots (Allen & Newhook 1973). Infection does not increase the proportion of occluded vessels in tap roots of jarrah seedlings (Davison & Tay 1987).

When large stems and roots are wound inoculated with *P. cinnamomi*, it preferentially colonises inner bark (Tippett *et al.* 1983; Davison *et al.* 1994). Although wound responses result in occlusion of xylem vessels adjacent to phloem lesions, this is of limited extent (Tippett & Hill 1984).

Field observations

Predictions for the field from the experimental work reviewed above are:

(i) if forest soil is waterlogged suddenly as a result of exceptionally heavy rainfall, the soil solution will rapidly become hypoxic and anoxic;

(ii) these conditions will not kill large jarrah roots, but will result in xylem vessels cavitating and becoming occluded with tyloses, so that these roots are less efficient at conducting water;

(iii) after the soil has drained, new functional xylem vessels will be formed by the root cambium. Thus, over time, the tylosed vessels in the sapwood will be replaced by newly formed vessels;

(iv) if there are seasonally high watertables in soil, large jarrah roots will be restricted to well aerated, surface horizons, so that jarrah trees on such sites will have shallow root systems;

(v) when the soil temperature is above 15°C and the matric potential is close to zero, *P. cinnamomi* sporangia will be formed on root lesions;

(vi) sporangia will not be formed below a watertable because aeration is inadequate, but will be formed in the moist soil above;

(vii) zoospores released from sporangia will move passively in percolating water through the profile into saturated soil where they will be attracted to, and infect, anaerobically respiring roots;

(viii) root infection will be more frequent in saturated soil than in moist soil;

(ix) the main tissue invaded will be the phloem;

(x) reduced hydraulic conductivity of root xylem will reduce the movement of water from the soil to the canopy, while increased infection of root phloem will reduce the movement of photosynthate and hormones from the crown to the roots;

(xi) both reduced hydraulic conductivity and increased infection will adversely affect tree growth.

Some of these predictions can be compared with field data.

Field measurements of perched watertables at Dawn Creek (Nanga Block) in June after 50 mm rain in the previous 4 days showed that the oxygen concentration of the soil solution was 49 per cent of water saturated with air (Davison & Tay 1991). Thus, perched watertables rapidly become hypoxic.

When jarrah dies on such sites, one would expect to find roots with large numbers of tylosed vessels in the sapwood, and extensively infected roots. Past investigations of jarrah deaths have included both anatomical and pathological studies (Table 1). Large numbers of tyloses were noted by Harding (1949), Stahl & Greaves (1959), Dell & Wallace (1981) and Davison (1993). *P. cinnamomi* lesions have not been found consistently, although failure by Harding (1949), Stahl & Greaves (1959), Podger (1968, 1972), Dell & Wallace (1981) and Shearer *et al.* (1981) to find lesions on vertical roots might be a result of incomplete root excavations (Table 1).

Table 1

Observations on tyloses and *Phytophthora cinnamomi* in jarrah trees.

Investigator(s)	Anatomical study		Pathological investigations	
		Tyloses noted	Consistent and extensive lesions	*Phytophthora* isolated
Harding (1949)	Yes	Yes	No	No
Stahl & Greaves (1959)	Yes	Yes	No	NA
Podger (1968, 1972)	NR	NR	NR	Yes
Dell & Wallace (1981)	Yes	Yes	Yes	Yes
Shearer, Shea & Fairman (1981)	NR	NR	Yes	Yes
Shea, Shearer & Tippett (1982)	NR	NR	Yes	Yes
Davison (1993)	Yes	Yes	No	No

NR, not reported; NA, not attempted

The most recent investigation of dying jarrah trees in a mass collapse site included the assessment of surface and sinker roots for both infection and tylosed sapwood (Davison 1993). No *P. cinnamomi* lesions were found. The mean proportion and standard deviation (calculated from arcsine-

Jarrah and understorey response to the introduction of *Phytophthora cinnamomi* on a well drained site

Jarrah and understorey response to the introduction of *Phytophthora cinnamomi* on an impeded drainage site
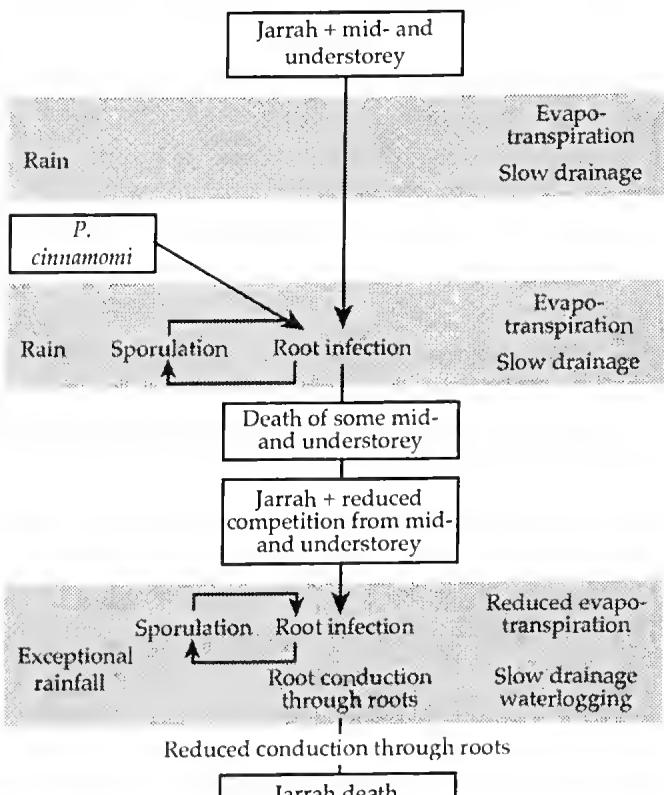
Figure 2. Hypothesised responses of jarrah and understorey to the introduction of *P. cinnamomi* on a well drained and an impeded drainage site.

transformed data) of tylosed vessels in 18 sinker roots was 74.8 per cent (standard deviation 44.2-96.3 per cent), and the mean proportion of tylosed vessels in 25 surface roots was 24.6 per cent (standard deviation 0.8-66.1 per cent). The proportion of tylosed vessel in the sapwood of surface roots from live trees from two other sites was 12.6 per cent (standard deviation 1.3-31.3 per cent, n=201), calculated from arcsine transformed data (Davison & Tay *unpublished data*).

Another prediction from experimental work is that there would be more lesions on roots of jarrah trees growing on poorly drained sites than on well drained sites. In excavations of apparently healthy trees growing on infested sites, Shearer & Tippett (1989) recovered *P. cinnamomi* from only 4.7 per cent of large roots. Similarly Davison & Tay (*unpublished data*) only found *P. cinnamomi* lesions on 3.4 per cent of 44 large roots from two sites which differed in soil drainage. In this latter study, lesions were too infrequent for statistical analysis.

Quite apart from its ability to infect jarrah, *P. cinnamomi* kills many mid-and understorey plant species (Podger 1968). By reducing vegetation density, it will reduce both interception of rainfall and evapotranspiration from the site (Greenwood *et al.* 1985). These changes will have a major effect on site hydrology, so that dieback sites will be wetter than adjacent uninfested areas. If site topography and/or soil profile characteristics result in poor drainage, this will be exacerbated by a removal of vegetation. Thus there will be an increase in both the incidence and duration of waterlogging on such sites in the occasional wet years (Fig 2).

Conclusions

In any investigation in plant pathology it is important to know as much about the host as about the pathogen. With studies of *P. cinnamomi* this may be conceptually difficult because this fungus has such a wide host range that it is natural to concentrate on the pathogen rather than on the many species affected, which in turn can affect the whole ecosystem. *Phytophthora cinnamomi* does not just infect plants, it also has a dramatic effect on site hydrology by reducing vegetation density. It is also important to consider how associated environmental factors affect the known physiological limitations of both host and pathogen because this may provide insights into how to predict when and where deaths will occur, and how to reduce their incidence.

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Ecological impact of plant disease on plant communities

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Abstract

Research, conducted in a range of plant communities, classified the susceptibility to plant pathogens of native plant species, including rare, threatened and poorly known taxa. The soil-borne pathogen *Phytophthora cinnamomi* and various canker fungi including *Botryosphaeria* spp. have had severe impact on a large number of plant species from south-west Australia. Over 38% of the 460 plant taxa surveyed were assessed as being susceptible to *P. cinnamomi*, while 59% of the 436 taxa examined show symptoms of significant canker activity.

The destruction of the many species susceptible to these diseases has had a serious impact on ecosystems in the south-west of Western Australia. The Proteaceae are most under threat from these fungi, with more than 86% of the species of Proteaceae assessed found to be affected by these pathogens. Almost all 233 species of Proteaceae listed as priority conservation taxa by Western Australia's Department of Conservation and Land Management are believed to be susceptible to *Phytophthora cinnamomi* and canker fungi. In large areas of south-western Australia, the Proteaceae are the most abundant plant group and so provide the fundamental elements of many plant communities. However, the Proteaceae are much less abundant at sites which have long been infested by *P. cinnamomi*, while plants which display low levels of susceptibility to the disease, such as sedge and rush species, are more abundant. The destruction of large numbers of proteaceous and other susceptible species may cause permanent changes in structure and function of plant communities.

Introduction

The degradation of plant communities by diseases is a serious problem in the south-west of Western Australia. These diseases pose an enormous threat to the flora of the south-west of Western Australia, which has been long recognised for its richness and its high degree of endemism (Hooker 1859; Diels 1906; Gardner 1944; Speck 1958; Hopper 1979). The Proteaceae and Myrtaceae are the most dominant families in the south-west, and especially in the kwongan, the shrubland vegetation common in the Northern Sandplain and the Southern Sandplain (*e.g.* George *et al.* 1979; Hopper 1979; Griffin *et al.* 1983; Hopkins *et al.* 1983; Lamont *et al.* 1984; Hopkins & Griffin 1984; Froend 1987; Wills 1989, 1993; Griffin *et al.* 1990); the Epacridaceae form a less substantial but omnipresent element. The Proteaceae in particular contribute most to species richness and projective foliage cover in many shrubland areas and so provide the fundamental floristic structure of many plant communities in south-western Australia. South-western Australia is home to about 618 species and subspecies of Proteaceae, by far the greatest concentration in the world; notably, this includes four endemic genera (Lamont, Wills & Witkowski, *unpubl. obs.*).

It is disturbing to note, therefore, that the Proteaceae in south-western Australia are very susceptible to diseases caused by a range of pathogens that include *Phytophthora cinnamomi*, various canker causing fungi, and *Armillaria luteobubalina*. We present here data on the impact of such diseases with emphasis on their effect on the Proteaceae.

Impact of *Phytophthora cinnamomi*

Phytophthora cinnamomi is principally a pathogen of woody perennial plant species, and herbaceous perennials, annuals and geophytes appear largely unaffected by the pathogen (Zentmyer 1980, Kennedy & Weste 1986, Podger & Brown 1989, Wills 1993, Websdane *et al.* 1994). Wills (1993) suggested that, based on research in the Stirling Range National Park, as many as 2000 of the 9000 native plant species in the south-west of Western Australia may be susceptible to *P. cinnamomi*. It was also reported that the majority of species from the Proteaceae, Epacridaceae, and Papilionaceae are susceptible to the pathogen (Wills 1993; also Table 1). Species of Myrtaceae are commonly cited as hosts for *P. cinnamomi* (*e.g.* Zentmyer 1980) but only a small proportion exhibit field susceptibility, and are generally of low susceptibility (Table 1; see also Podger & Brown 1989, Wills 1993).

In field studies of southern plant communities, 92% of the family Proteaceae were rated as susceptible to the introduced soil-borne pathogen, *P. cinnamomi* (Table 1). When this fungus invades communities dominated by proteaceous species, and particularly *Banksia* or *Dryandra*, substantial

Table 1
Summary of data on canker and dieback available for key families

	Susceptible	Total Rated	%
Dieback - general	177	460	38
Proteaceae	101	110	92
Myrtaceae	16	97	16
Epacridaceae	20	25	80
Papilionaceae	13	23	57
Canker - general	273	436	59
Proteaceae	120	139	86
Myrtaceae	62	99	63
Epacridaceae	11	32	34
Papilionaceae	28	49	57

changes in plant abundance and in floristic structure of plant communities may be observed (Table 2). These changes have been reported in other studies of Proteaceae-dominated communities (Weste 1981, Kennedy & Weste 1986, Shearer & Hill 1989, Hill 1990, Shearer & Dillon 1994).

Table 2

Numbers of taxa susceptible to *Phytophthora cinnamomi* and various canker fungi compared with total number assessed, and percentage difference in cover of species in 10 m x 10 m plots at healthy and old-infested dieback (>10 years) sites, and immediate impact of canker on live cover compared with total cover. (numbers of species in plots given in brackets) Cover for *Grevillea* omitted due to small sample size.

	Number Susceptible	Number assessed	% difference in cover	
Dieback				
All taxa	177	460	29	(191)
Proteaceae	101	110	72	(47)
Banksia	29	29	93	(8)
Dryandra	15	15	79	(10)
Grevillea	2	6	-	
Hakea	16	20	52	(11)
Isopogon	12	12	72	(5)
Petrophile	9	9	69	(6)
Canker				
All taxa	273	436	14	(230)
Proteaceae	120	139	25	(60)
Banksia	27	29	17	(12)
Dryandra	15	17	33	(9)
Grevillea	10	11	26	(3)
Hakea	29	32	31	(16)
Isopogon	9	10	28	(4)
Petrophile	13	13	19	(6)

Impact of canker fungi

In recent years, a new fungal threat has emerged. Several aerially-dispersed, canker-causing fungi have been found in a taxonomically diverse group of native plants from many plant communities in south-western Australia. These include a number of taxa classified as vulnerable or endangered (Murray *et al.* 1994, Shearer 1994). The cankers, including species of *Botryosphaeria* and *Diplodina*, have caused extensive damage to large stands of vegetation in south-coastal areas of Western Australia (Shearer & Fairman 1991a, Wills 1991, Bathgate *et al.* 1994, Khangura *et al.* 1994, Murray *et al.* 1994, Shearer 1994), particularly since February 1991 (Wills 1991). It appears likely that unusual weather conditions, comprising 6 months of serious rainfall deficiency up until May that year, and a heat-wave lasting four days and reaching 47°C, contributed to the rapid growth of the cankers observed since that time in native plant communities. Extensive plant death has also been recorded as a result of periods of drought (Hnatiuk & Hopkins 1980), but the symptoms associated with the drought deaths (A J M Hopkins, *pers. comm.*) are distinct from those of canker impact.

Surveys on the Southern Sandplain (Wills 1991) and in the south-west (Murray *et al.* 1994) reveal that 59% of species assessed from a range of families were affected by canker fungi (Table 1). About 86% of Proteaceae were damaged and frequently killed by canker fungi (Table 2), although the level of damage sustained by different species was extremely variable. However, some species suffered severe impact with large stands being destroyed *e.g. Banksia coccinea* and *B. baxteri.* These species are restricted to south coastal areas of Western Australia and are both highly susceptible to damage by canker fungi. As a result, the commercial picking of infloresences from wild populations of these species has now been banned (see Wills & Robinson 1994).

Impact of *Armillaria luteobubalina*

Armillaria luteobubalina has a broad host range and is widespread in jarrah, karri, tuart and wandoo forest as well as woodlands and shrublands throughout the south-west of Australia (Shearer 1994). For example, in coastal dune shrubland communities 307 plant species were recorded in the sites assessed, and 112 of these were hosts to *A. luteobubalina.* (Shearer *et al.* 1994). Susceptible species were mainly from the Proteaceae, Myrtaceae, Epacridaceae, Papilionaceae and Mimosaceae; the species killed included the geographically restricted *Callitris preissii* (itself forming a rare community), and rare and endangered *Banksia brownii* and *B. occidentalis formosa* (Shearer *et al.* 1994).

Ecological consequences

Changes in community structure following infestation are inevitable because virtually all species susceptible to *P. cinnamomi* and the majority of species susceptible to canker fungi and *A. luteobubalina* are woody perennials, while many field resistant species are herbaceous perennials. While even highly susceptible species are generally not eradicated with the initial invasion of the fungi, the abundance of susceptible species can be greatly reduced. At sites with a longer exposure to *P. cinnamomi*, susceptible species may eventually be eliminated (Wills 1993); the same outcome may result from the activity of the other two diseases. Evidence for some regeneration of susceptible species at long-infected sites has been found (Weste & Ashton 1994), but it appears unlikely that susceptible species would return to previous levels of abundance, and changes in isolated remnants lacking extant seed sources will probably be irreversible (see Keighery *et al.* 1994) without intervention.

In the case of *P. cinnamomi*, the fungus causes not only the decline in species richness of susceptible species at a site, but also a change in plant community structure and biomass as field resistant species, especially herbaceous perennials, become more abundant. These changes may translate into indirect losses in community productivity due to changes in plant biomass and degrade the capacity of infested sites to support dependant biota.

Changes in habitat due to the alteration of community structure and composition may impact plants not affected by the disease. For example, most species of the Stylidiaceae appear to be field resistant to *P. cinnamomi*. However, one species (*Stylidium scandens*) is common in healthy sites in the Stirling Range National Park but absent in adjacent areas with a high disease impact. It seems likely that this species, which grows in dense understorey below stands of *Eucalyptus marginata*, may disappear as the structure of the stand is opened up through the loss of shading canopy and the death of susceptible understorey species. Other species with specific habitat requirements may suffer similar indirect effects of the pathogen or may benefit from such changes. For example, introduced annual species invade more readily after disturbances (Hobbs & Atkins 1988), and introduced annuals have been shown to increase in abundance following the removal of the canopy of dense native plant communities (Hobbs & Atkins 1991). This may be particularly important given that most annual species may be field resistant to *P. cinnamomi* (Podger & Brown 1989; Wills 1993), a factor that may enhance the invasibility of sites infested with the pathogen. Furthermore, if annuals become abundant, regeneration by native perennials is likely to be severely inhibited (Hobbs & Atkins 1991).

Changes in the availability of resources and in habitat due to the alteration of community structure and composition may affect associated groups of animals *e.g.* pollinators, grazers (Wills 1993, Wills & Kinnear 1993, Laidlaw & Wilson 1994, Newell 1994, Wilson *et al.* 1994) and soil biota (Malajczuk 1979, Malajczuk & Pearce 1994).

The disturbance of pollinators can have serious implications for plant communities. For example, almost all wind-pollinated species appear to be unaffected by diseases caused by *P. cinnamomi* or canker fungi. In contrast, the majority of vertebrate-pollinated species assessed are affected by these pathogens, in part a reflection of the prominence of vertebrate pollination in the Proteaceae. Pollinators reliant on susceptible plant species as key nectar sources (*e.g. Banksia*) may become rare or locally extinct in old-infested areas. Reduction in the population size of pollinators could affect the stability and viability of breeding populations and may result in the local extinction of the animal species at a site. This may be compounded by physical changes to the habitat, especially in cases where monocotyledons such as sedges colonize the spaces created by the loss of susceptible plants. In addition, it is possible that a reduction in the number of pollinators could affect the reproductive success of surviving plants, further contributing to a decline in community structure and ecosystem viability.

Threatened taxa

While emphasis in the above discussion has been on the keystone species, there are rare and vulnerable species that are also at risk (Table 3). Notably, when all rare and vulnerable species from the south coast considered most at risk from dieback and/or canker are ranked, all but one of the species considered under greatest threat from plant diseases are proteaceous (Table 4). For example, the only known population of *Dryandra* sp. (Kamballup) is infected with canker (D L Murray & R T Wills *unpublished*), and all known populations of *Banksia brownii* are infected with *P. cinnamomi*. Needless to say, other species from other families are also at considerable risk (*e.g.* see Lemson 1994). Furthermore, these diseases threaten the survival of animals, as exemplified by the impact of *Armillaria* that kills broom bush (*Choretrum glomeratum*), the only food plant of the larvae of a rare species of butterfly, *Ogyris otanes* (Wills & Kinnear 1993).

Table 3
Summary of 494 out of 1655 Declared Rare Flora and Priority taxa ranked for their susceptibility to dieback and/or canker.

	Susceptible	Total Rated	%	Total priority
Priority Species				
Dieback	307	494	62[a]	1655
Proteaceae	205	213	96	213
Myrtaceae	1	91	1	334
Epacridaceae	(68)[b]	68	—[b]	68
Papilionaceae	24	26	92	92
Priority Species				
Canker	322	353	91[a]	1655
Proteaceae	213	213	100	213
Myrtaceae	8	12	75	334
Epacridaceae	(68)[b]	68	—[b]	68
Papilionaceae	25	26	96	92

[a] Biased sample due to ratability

[b] Impact variable - all species currently rated as susceptible

Table 4
Taxa from the south coast considered most at risk from dieback and/or canker.

Species	Conservation Status[c]	Susceptibility Dieback	Canker
Lambertia orbifolia	E	High	High
Andersonia sp.[a]	E	High	Moderate
Banksia brownii	E	High	Moderate
Banksia verticillata	E	High	Moderate
Adenanthos linearis	2	High	Moderate
Banksia occidentalis subsp. *formosa*	2	High	Moderate
Dryandra sp.[b]	E	High	High
Isopogon uncinatus	E	High	High
Lambertia echinata subsp. *echinata*	E	High	High
Lambertia fairallii	E	High	High
Isopogon alcicornis	2	High	High

[a] Two Peoples Bay (GJK 8229)

[b] Kamballup (M Pieroni 20.9.88)

[c] E=endangered; 2=CALM priority 2 taxon; few poorly known populations on conservation lands.

Disease amelioration

Currently, the most practical management technique for the control of *P. cinnamomi* in native plant communities is foliar application of the fungicide phosphonate, "phosphorous acid" (Shearer & Fairman 1991b, Komorek *et al.* 1994, Hardy *et al.* 1994). Field trials in various areas in the south-west on plant communities already infested with *P. cinnamomi* have shown that one application of phosphonate gives excellent control of the disease over several years (see review article by Hardy *et al.* 1994).

While canker fungi are not a major problem in south-western Australia, they are distributed throughout this region and have the potential to cause very serious damage. Fire is the most practical management tool for the regeneration of native plant communities after infestation by canker.

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Smut and root rots on native rushes (Restionaceae) and sedges (Cyperaceae)

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Abstract

Native rushes (Restionaceae) and sedges (Cyperaceae) are widespread and common components of the vegetation of south-west Western Australia. In phytopathological terms many taxa within these families are susceptible to indigenous smut diseases, which affect culms and reproductive organs, yet are apparently resistant to habitat invasions by *Phytophthora* species. Smut disease has been found in a quarter of the 113 species of Restionaceae, representing 11 out of the 19 genera for the State, and in 17 species and 9 genera of Cyperaceae. For many species, smut diseases result in total loss of viable seed production. Culm smut has been recorded in only one species, and in this case infection results in retardation in growth and development of culms and reduced seed output. Conversely, introduced *Phytophthora* species have limited impact on survival and reproduction of native Restionaceae. Controlled inoculation of *P. cinnamomi* shows that disease symptoms are confined to localised regions on the roots, with a limited degree of cross infectivity between roots. Infected roots of test species produce abundant, healthy lateral roots above the lesions and symptoms in shoots are not apparent. The use of Restionaceae as barrier plantings for containing infection to sites within a habitat or protecting sites of rare taxa which are susceptible to *P. cinnamomi* is presently being investigated. An understanding of the diseases of rushes and sedges is important for the management of these plants in natural communities and in horticultural enterprises.

Introduction

Until recently, the effect of disease on Restionaceae has been limited to taxonomic description of species of smut (Ustilaginales) on host plants (McAlpine 1910) and the increase in rush and sedge abundance in wild sites affected by *Phytophthora* (Wills 1993). Many smuts have been described on the closely related Cyperaceae and the impact of *P. cinnamomi* on sedges has been studied in eastern Australia (Weste 1986; Phillips & Weste 1984; Cahill *et al.* 1989).

Southern-hemisphere rushes and sedges are widespread and common components of the flora of south-west Western Australia. They inhabit a wide range of the northern sand plains, coastal wetlands and to a lesser extent the jarrah forest. Most species are long-lived perennials, with culms initiated from an underground rhizome in late autumn to early winter. Most Restionaceae are dioecious, with a few monoecious and hermaphroditic species, while sedges are monoecious. All species of both families flower from early winter to early summer, are wind pollinated, with most species producing very few viable seeds which are short lived and germinate in response to soil disturbance (Meney & Dixon 1988, Meney *et al.* 1994). Taxa can be classified into two broad groups, seeders and resprouters, depending on their reproductive and vegetative biology, and their response to disturbances, such as fire. Their life strategies occur along a continuum from fire sensitive seeders, recruiting from seed after fire, to resprouters which regenerate

from heat resistant or deeply buried perennating buds located on the rhizome (Pate *et al.* 1990).

An understanding of the impact of *Phytophthora* and smuts on native rushes and sedges is critical, as many species are harvested extensively from natural populations for use in the floriculture industry. Many species are also important in rehabilitation of mining areas due to the sand-binding nature of their roots (Pate & Dixon 1994) and dominance in pre-mined vegetation (K Meney *pers. comm.*).

Impact of smut on native rushes and sedges

McAlpine (1910) described smuts on nine sedge species and two rush species from Eastern Australia. He wrote of the Western Australian smuts, "Only those species are known which attack cultivated crops and those occurring on the native flora are yet to be discovered". In the last seven years, 43 rush and sedge species in 20 genera have been recorded as smut hosts in Western Australia (Table 1). These smuts are as widespread as their hosts and represent the most debilitating pathogens of rushes and sedges. Thus, smut impacts are likely to play a significant role in rehabilitation and conservation of these families in the future.

Taxonomy

The taxonomy of smuts is based on spore morphology, mode of spore germination and specialisation at host genus level. There are about 43 new species among these smuts and their taxonomy is currently under investigation. With the exception of one smut, all sporulate in inflorescences and have affinities to *Tolyposporium*. One species, *T. restionum*, has recently been described on a native rush *Alexgeorgea*

nitens (Nees) L Johnson & B Briggs (Websdane *et al.* 1994). The exception to the inflorescence smuts is the culm smut *Ustilago lyginiae* (Websdane *et al.* 1993) on *Lyginia barbata* (Labill) R Br. This is the first record of a culm smut on Restionaceae.

Table 1
Recorded hosts of smuts within Restionaceae and Cyperacea in Western Australia

Restionaceae		Cyperaceae	
Genus	Species	Genus	Species
[1]*Alexgeorgea*	*A. nitens*	[4]*Carex*	*C. fascicularis*
	A. subterranea		
		[6]*Caustis*	*C. petandra*
[3]*Anarthria*	*A. laevis*		
		[3]*Cyathochaeta*	*C. avenacea*
[3]*Desmocladus*	*D. biformis*		*C. clandestina*
	D. elongatus		
	D. flexuosus	[3]*Evandra*	*E. aristata*
[3]*Harperia*	*H. confertospicatus*	[5]*Isolepis*	*Isolepsis sp.*
[3]*Hypolaena*	*H. fastigiata*	[3]*Lepidosperma*	*L. angustatum*
	H. macrotepala		*L. effusum*
			L. gladiatum
[3]*Lepidobolus*	*L. chaetocephalus*		*L. gracile*
	L. deserti		*L. Longitudinale*
	L. preissianus		
		[3]*Mesomalaena*	*M. gracileps*
[3]*Leptocarpus*	*L. aristatus*		*M. pseudostygia*
	L. ceramophilus		*M. stygia*
	L. elegans		
	L. scariosis	[3]*Shoenus*	*S. laevigatus*
			Schoenus sp.
[3]*Lepyrodia*	*L. macra*		
		[3]*Tricostularia*	*T. neesii*
[2,3]*Lyginia*	*L. barbata*		
[3]*Pseudoloxocarya*	*P. magna*		
[3]*Restio*	*R. chaunocoleus*		
	R. isomorphus		
	R. leptocarpoides		
	R. microcodon		
	R. sinuosa		
	R. sphacelata		
	R. stenandra		
Totals	26	17	

Identity of smuts associated with host taxa.

[1]*Tolyposporium alexgeorgii.*
[2]*Ustilago lyginiae* (culm smut).
[3]Tentatively identified as *Tolyposporium* species (inflorescence smuts).
[4]Tentatively identified as *Farysia* species.
[5]Tentatively identified as an *Anthracoidea* species by R Shivas
[6]Unidentified

Symptoms

The symptoms of inflorescence smuts are not always obvious, as the spore mass or sorus is generally enclosed in the inflorescence. In Restionaceae, smut infections manifest as massive sporulation by the fungus in the ovaries (Fig 1-1) and anther sacs of inflorescences. Infection results in partial to total loss of seed productive capacity. In the monoecious Cyperaceae, the sorus surrounds developing anthers and stamens rendering them sterile.

Transvestism is an interesting abnormality observed in several dioecious rush species affected by smuts. For example, when smutted the normally pendulous male inflorescences of *Restio microcodon* L Johnson & B Briggs take on the appearance of healthy, erect female inflorescences (Fig 1-2). Thus, in transvestite-susceptible species, partial smutting results in male plants appearing to be hermaphroditic. Indeed, transvestism in smutted male inflorescences of *A. nitens* led to its misidentification by Nees (1846). The nor-

mally tufted inflorescences (Fig 1-3) become swollen when smutted (Fig I-4) and, according to Nees, resembled inflorescences of female *Restio* species. Nees called the host species *R. nitens* and mistook the smut for a rust which he named *Uredo restionum.* Johnson & Briggs (1896) resolved this misidentification and clarified the taxonomic identity of the host. The identity of the pathogen has also been clarified recently as *T. restionum* (Websdane *et al.* 1994).

In certain other host species examined, the only evidence of smut infection was a slight swelling of the host inflorescence and in many sedges smutted spikelets cannot be distinguished from those which are healthy.

The culm smut recorded on *Lyginia barbata* is easily recognised as a raised, brown, crust-like structure, or peridium, derived from host epidermal cells, which encloses the powdery spore mass (Fig 1-6). These spores have high viability, germinate readily and survive for at least one year and possibly longer. Spores of inflorescence smuts on the other hand appear to have either a long period of dormancy or a short period of viability and spores of most of these smuts have not been successfully germinated. The development of the culm smut sorus occurs during culm growth and well before inflorescence initiation. The sorus prevents further development of culms eventually causing dieback of culm apices. Thus all infected culms are sterile (Fig 1-5; Websdane *et al.* 1993).

Disease impact

Smuts often fully replace the reproductive structures of host plants and render the plants sterile. In many seeder species, smut infection causes total loss of reproductive capacity in infected plants. Field observations on the resprouter species *A. nitens* indicate that smut infection is systemic via the ramifying rhizome system. This was shown by tracking rhizomes from smutted parent plants to underground buds and enclosing developing buds in spore-proof glassine bags. At inflorescence maturity all new plantlets originating from smut infected parent plants were also infected, indicating systemacy (K Websdane, *unpublished data*).

Disease incidence

Smuts have been found on hosts from isolated, undisturbed habitats. For example, a population of *Lepidobolus deserti* Gilg was found to have less than 1% smutting at the Queen Victoria Springs on the edge of the Great Victorian Desert. It appears however that disturbance exacerbates the disease incidence as 20 to 50% smutting has been recorded in populations experiencing frequent fires, mining activities or road works (K Websdane, *unpublished data*).

Implications of smut disease for conservation and restoration

Smut infection is likely to be a problem in post-mining situations where successful restoration of species of rushes and sedges is dependent on creating self-sustaining populations of plants producing seed and healthy seedlings. For example, smutted plants of *Lepidobolus chaetocephalus* Nees, a seeder species, experience up to 100% loss of seed production in sites adjacent to mining areas in northern
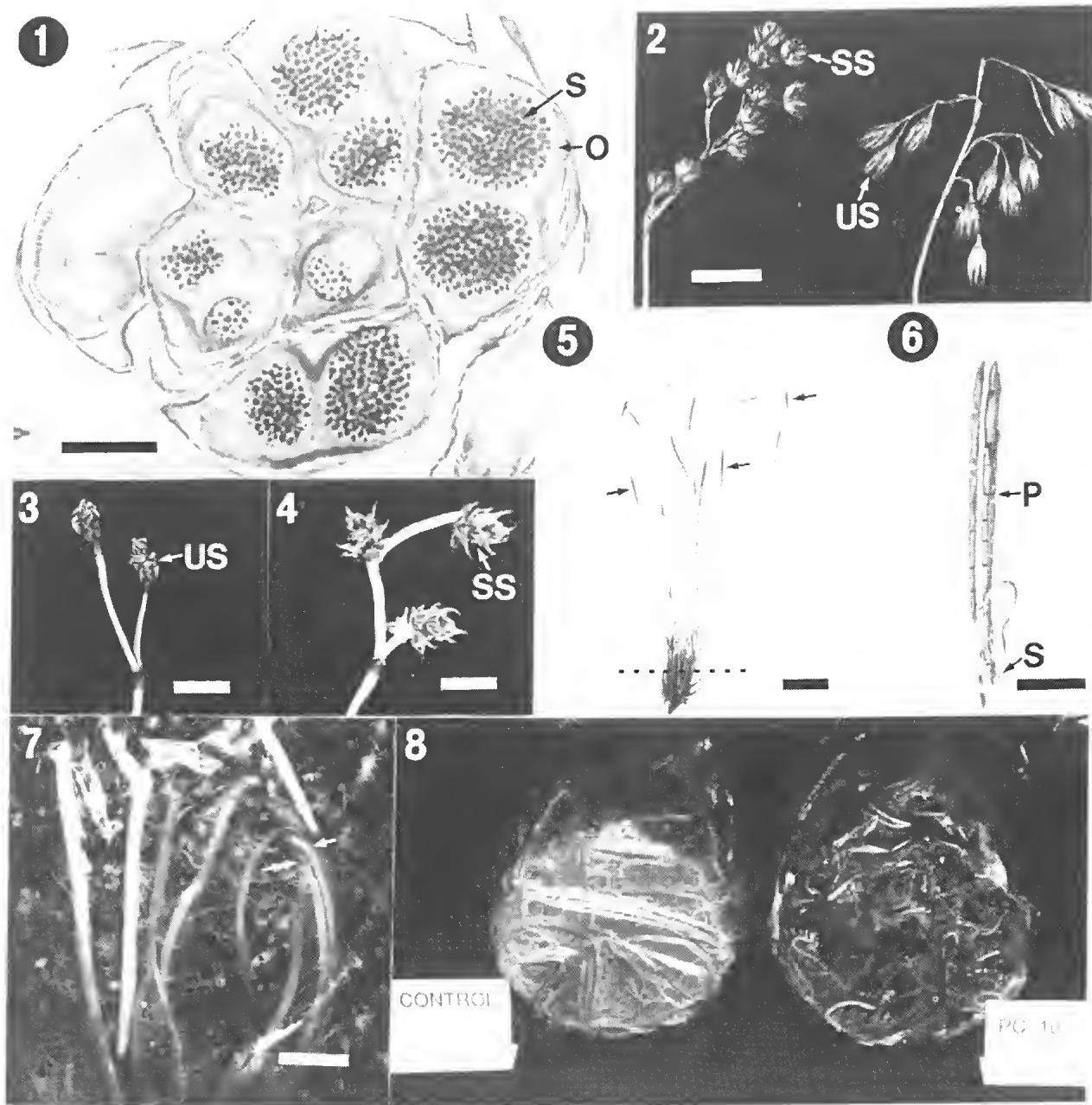
Figure 1. 1. Cross-section of female *R. microcodon* spikelet showing the production of smut sori in ovaries, preventing seed production. S=sorus O=ovary wall (bar=1mm). 2. Smutted spikelets (SS; left) and uninfected spikelets (US; right) of a male *R. microcodon* plant. Smutted male spikelets appear identical to healthy female spikelets (bar=1cm). 3. Uninfected spikelets (US) of a male *A. nitens* plant (bar=0.5cm). 4. Smutted spikelets (SS) of a male *A. nitens* plant thought by Nees (1846) to resemble female spikelets of *Restio* species (bar=0.5cm). 5. Whole plant of *L. barbata* infected by *U. lyginiae* (culm smut) showing sori (arrows) (bar=5cm). 6. Close-up of culm smut sori along a culm of *L. barbata*. P=peridium. S=scale leaf. (bar=1cm). 7. Roots of *Loxocarya magna* root rot symptoms. Healthy lateral roots (arrow) are initiated above water soaked lesions (double arrow) (bar=2cm). 8. The difference in root mass, at the base of the pot, between control and inoculated plants of *Loxocarya magna*.

Kwongan regions. This has serious implications for the survival of this species in rehabilitation programs. This host relies on current season seed production for seedling recruitment after fire, rather than soil seed banks (Meney 1993). Thus, a high incidence of smut infection and fire can result in death of parent plants and dramatically reduced seedling recruitment. These factors, in addition to high levels of seedling mortality recorded for this species (Meney *et al.* 1994), may result in localised extinction of this species (K Websdane, *unpublished data*).

Of the 17 rush and sedge species harvested from the wild for the cut-flower industry, half have been recorded as hosts for smuts. In a number of these species infection of inflorescences is diagnosed only after careful examination. This means that smutted inflorescences could unknowingly be harvested along with those which are healthy. The disease is therefore likely to have an impact on the sustainability of bush harvesting and on product quality particularly for export markets. It is critical for pickers to be aware of the disease in order to recognise and avoid smutted plants and populations and prevent the export of diseased material around the world.

Impact of *Phytophthora cinnamomi* on native rushes and sedges

Since the invasion of *P. cinnamomi* into the sclerophyll forests of Australia there has been a marked reduction in the diversity of understorey species present in infested sites (Weste 1986, Wills 1993). Members of the Epacridaceae and Proteaceae which are highly susceptible to the pathogen have been replaced by monocotyledons, especially members of the Restionaceae and Cyperaceae. Within the Stirling Range National Park a greater number of Restionaceae species were recorded in old-infested sites than healthy sites and their percentage cover increased significantly from four percent in healthy sites to ten percent in old-infested sites, with a similar increase in the abundance and frequency of Cyperaceae in long term, diseased sites (Wills 1993). The dominance of these species in diseased areas has been attributed to their field resistance to *Phytophthora* root rots.

Previous research showed *P. cinnamomi* to infect the roots of three species of sedges from the Brisbane Ranges in Victoria (Phillips & Weste 1984, Cahill *et al.* 1989), however only field observations have been made on the field resistant nature of the Restionaceae. The resistance of two species of Restionaceae to increasing levels of *P. cinnamomi* inoculum was studied under glasshouse conditions. Clonally propagated plants of *Loxocarya magna* Meney & Dixon (ined) and *Restio amblycoleus* F Muell were inoculated with *P. cinnamomi*. Examination of the roots eight weeks later showed the development of water-soaked lesions immediately behind the root tip but new lateral roots formed above these lesions and limited cross infection was apparent (Fig 1-7; Sieler *et al.* 1993). Inoculated plants of *L. magna* produced a greater number of thick, depth-seeking roots and fewer bifurcated laterals than control plants (Fig 1-8). There were no symptoms in the above-ground portion of the plants except for some yellowing of juvenile leaves and culm tip die-back in some treatments. Production of new reproductive culms was high for all inoculated plants, with a greater number of new culms being produced at high levels of inoculum. The ability of these plants to produce new roots and reproductive culms once infected has important implications for the rehabilitation of affected sites and the management and recovery of rare species of rushes and sedges.

At least 11 species of rare and endangered or priority rushes and sedges are located in areas infested with *P. cinnamomi*. The potential benefits of field resistance in rushes and sedges is considerable including reinforcement and reintroduction into disease affected areas. In addition, species such as *R. ustulatus* (F Muell ex Ewart & Sharman) L which is both a priority species and recorded as being harvested, may be used in the reclamation of sites or high risk horticultural sites as an alternative to bush picking.

The use of rushes and sedges to act as biological barriers to reduce the impact and rate of spread of *P. cinnamomi* is currently being investigated. Phillips & Weste (1989) showed zoospores to be produced from infected roots of the sedge *Gahnia radula* but the potential of infected roots to act as a future source of inoculum is not known. In a study of the barrier potential of Restionaceae to *P. cinnamomi*, adult plants of *R. amblycoleus* were placed into the middle of pots divided into three portions with Mira cloth (Calbiochem. Corp, La Jolla, USA). *Banksia* seedlings were planted on either side of

the rushes and one set of plants inoculated with *P. cinnamomi*. In comparison to control pots, banksias in pots containing rushes showed a mark reduction in disease presence and delayed movement of inoculum. Passage of *P. cinnamomi* through the soil occupied by roots of a rush has been slow, and studies are continuing to determine the effectiveness of the Restionaceae as a biological barrier to the movement of the pathogen through soil.

Conclusions

Although there is a great diversity of flora in Western Australia, phytopathological studies have concentrated on those components which are most visibly affected by pathogens. In contrast to the timber and highly floriferous species, only limited work on disease impact and interactions has been conducted on the Cyperaceae and Restionaceae. Their importance in floriculture and rehabilitation of mine sites, *Phytophthora* affected areas or high risk horticultural sites indicates a more economic role for these families in the future and the need for on going research.

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Impact of plant diseases on faunal communities

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Abstract

Plant pathogens can have a major effect on vegetation floristics and structure. Effects include loss of plant species, decline in vegetation cover, and an increase in bare ground and the abundance of resistant plant species. These changes would be predicted to affect the faunal communities inhabiting infected habitats, but there have been few studies which examine the relationship between faunal abundance and composition and plant pathogens. This paper considers the potential affects of plant pathogens on faunal communities and reviews recent work on the effects of *Phytophthora cinnamomi* (cinnamon fungus) on mammals and invertebrates. Analysis of a number of disturbance factors in heathland and woodlands of south-eastern Australia have identified *P. cinnamomi* infection as being associated with low species richness, and low abundance of small mammals. Studies on populations of *Antechinus stuartii* (brown antechinus) in woodlands found that there were lower capture rates, and habitat utilisation was altered. The major contributing factor was alterations to vegetation structure, rather than food availability. In heathlands, species such as *Rattus lutreolus* (swamp rat), *Rattus fuscipes* (bush rat) and *Antechinus stuartii* were found to be less abundant in areas infected with *P. cinnammomi*.

Introduction

The habitat and microhabitat preferences exhibited by animal species are determined by a number of basic requirements such as the provision of adequate food resources, the presence of cover (protection from predators, suitable microclimate) and access to breeding, basking or roosting sites. Vegetation attributes make a major contribution to these habitat components. For example, understorey vegetation and litter provide important refuges and breeding areas for invertebrates. Omnivorous or herbivorous terrestrial lizards are dependent on vegetation as foraging sites, while some species require elevated sites for thermoregulation. Birds require vegetation for nest sites, some using tree cavities, others shrub or dense ground vegetation, and most species also depend on vegetation for food such as nectar, seeds, fruit or invertebrates. Small terrestrial mammals depend on vegetation for cover, food and protection. Tree bark, litter and woody debris, harbouring a diverse range of invertebrates, also provide foraging sites for insectivores.

Studies have provided evidence that small mammals exhibit microhabitat selection based on vegetation characteristics (Braithwaite & Gullan 1978, Braithwaite *et al.* 1978, Cockburn 1978, 1981, Fox & Fox 1981). Analyses of factors found that structural attributes of vegetation were important indicators for habitat preferences for some species (Barnett *et al.* 1978, Stewart 1979, Newsome & Catling 1979), while for others both floristic and structural characteristics were significant (Braithwaite & Gullan 1978, Braithwaite *et al.* 1978, Fox & Fox 1981). For example, a number of pseudomyine rodent species exhibit preferences for diverse floristic communities, which are likely to be related to dietary requirements (Braithwaite & Gullan 1978, Cockburn 1978, 1981, Fox & Fox 1981, 1984). Species such as the omnivorous bush rat (*Rattus fuscipes*) respond mainly to structural factors while the herbivorous swamp rat (*Rattus lutreolus*) has a requirement for a sedge food resource (Braithwaite *et al.* 1978, Barnett *et al.* 1978).

Plant pathogens can have a major effect on vegetation communities. They may decrease the fitness of individual plants, alter the size and genetic structure of individual populations and thus the structure and diversity of whole plant communities (Burdon 1991). There may also be a range of effects from pathogens depending on the intensity of the pathogen and the conditions present at the time of infection. The consequences for animal habitats will also vary according to the intensity of pathogen effects and the percentage of resistant plants present. In some cases, marked changes to habitat conditions may occur if the pathogen affects all the vegetation present, or if there is total mortality of susceptible species. Indeed, some pathogens lead to almost complete loss of plants present, from the understorey to the canopy. In other situations only understorey vegetation may be affected. Thus, animals that rely on different habitat components would be affected differentially. For example, arboreal marsupials (*e.g.* folivores, nectarivores) and many bird species are likely to suffer as the consequence of canopy damage. Terrestrial mammals and invertebrates would be seriously affected if all understorey vegetation is eliminated. Furthermore, some animal species are reliant on particular plant species for their food. If those plant species are highly susceptible to a pathogen, then this will have important consequences for animal food resources.

In this paper we examine evidence and recent research on the impact of a particular plant pathogen, cinnamon fungus (*Phytophthora cinnamomi*) on fauna. We assess the affects of *P. cinnamomi* on vegetation together with consequential

effects on animal populations, communities, habitats and diet. The role of *P. cinnamomi* as a disturbance regime in native communities is examined, and the long-term consequences of infestation and resilience of these communities is assessed.

Effects of *P. cinnamomi* on vegetation and animal habitats

The fungal pathogen *P. cinnamomi* causes extensive "dieback" of Australian native vegetation. It is widespread and occurs in forests ranging from the jarrah forests of Western Australia to the stringybark and silvertop ash forests of Victoria, and the tropical rainforests of Queensland. It also occurs in woodlands and heathland communities *e.g.* the Grampians and Brisbane Ranges, in Victoria and in Western Australia (Newhook & Podger 1972, Podger & Ashton 1970, Weste & Taylor 1971, Weste 1974, Wills 1993).

The pathogen has a wide host range, although its pathogenicity to different hosts varies, and its growth and distribution are influenced by tempereture, soil type, nutrient status and water availability (Weste & Marks 1987, Marks & Smith 1991). Hence the expression of the disease varies from site to site. Studies of infected vegetation have shown that *P. cinnamomi* has a major effect on the understorey, and up to 60% of the plant species present have been eliminated after infection (Weste 1974, Dawson *et al.* 1985, Kennedy & Weste 1986, Wills 1993). Infection results in decreases in seedling regeneration, species diversity and the population density of species (Weste 1986, Dawson *et al.* 1985, Kennedy & Weste 1986), but there is often an increase in the frequency & Weste 1986), but there is often an increase in the frequency & cover of field resistant monocotyledons (Dawson *et al.* 1985, Weste 1986, Kennedy & Weste 1986). In severely affected areas, the understorey community has been changed from diverse sclerophyll to a sedge-dominated understorey, due to the resistance of sedges to *P. cinnamomi*. In some situations large areas have become denuded of vegetation, often resulting in severe erosion (Kennedy & Weste 1986).

The changes in vegetation communities associated with *P. cinnamomi* infection would be predicted to affect the fauna present (Table 1). Decreased canopy cover could potentially affect nesting birds and arboreal marsupials, while simplification of the understorey vegetation may affect sources of seed, nectar and pollen available for mammals, birds and insects. Indeed, species such as the honey possum (*Tarsipes rostratus*), which rely entirely on a specialized diet of pollen and nectar mainly from highly susceptible proteaceous species (*e.g.* Banksias), are likely to be severely affected by *P. cinnamomi* (Friend 1992).

Alterations to understorey vegetation and litter could alter habitat conditions for invertebrates. Thus, one may expect changes in the abundance and composition of invertebrate communities which in turn influence the diets of insectivorous animals such as small dasyurid marsupials. Dibblers (*Parantechinus apicalis*), for example, were rediscovered in 1967 at Cheyne Beach on the south coast of Western Australia (Morcombe 1967), and shown to forage on invertebrates which inhabited the wildflowers and deep litter layer characteristic of the site. Since that time, this habitat has been severely affected by both *P. cinnamomi* and the canker fungus *Diplodonia* spp., and the status of *P. apicalis* in this area is uncertain. Like the honey possum, the dibbler is potentially under great threat from *P. cinnamomi* and other pathogens.

Table 1
Predicted effects on fauna due to the presence of *P. cinnamomi* (cinnamon fungus) in vegetation communities.

Effects on vegetation	Effects on fauna
1. Loss of susceptible plant species in the understorey, midstorey	a) Direct loss of food sources *e.g.* seeds, nectar, pollen. b) Indirect loss of food sources *e.g.* invertebrates.
2. Decline in plant species' richness and diversity	a) Loss of food for species that prefer floristically rich vegetation. b) Loss of seasonal food availability.
3. Decrease in plant cover, increase in bare ground, erosion.	a) Loss of habitat for species dependant on thick ground cover. b) Increased predation risk. c) Changes to microclimate conditions.
4. Decrease in canopy cover	a) Loss of food for arboreal species. b) Loss of habitat for arboreal species.
5. Decrease in litter fall.	a) Decline in litter invertebrates (dry conditions) b) Decline in invertebrate food sources for insectivores.
6. Post infection increase in frequency of field resistant plant species *e.g.* sedges.	Increase in food for specialist herbivores

Species such as the pseudomyine rodents have been shown to be dependent on floristically-diverse understorey (Cockburn 1978, Cockburn *et al.* 1981, Fox & Fox 1984) and are potentially endangered by the simplification of diverse sclerophyll communities resulting from *P. cinnamomi* infection. By contrast, animals with relatively generalized diets that require dense, low vegetation for shelter may prefer habitat that has been infected by *P. cinnamomi*, if there has been a consequent increase in the cover of field resistant monocotyledons. In severely affected areas, decreases in plant cover could lead to loss of habitat or a decline in the carrying capacity for these animals.

Effects of *P. cinnamomi* on animal populations

Although there have been a substantial number of studies on the effects of *P. cinnamomi* on vegetation (see review by Weste & Marks 1987), there has been little work investigating the less direct effects of the pathogen on faunal populations and communities.

Two studies have compared invertebrate communities in healthy and infected jarrah forests in Western Australia. Postle *et al.* (1986) found that infected jarrah forest had 48% less litterfall, and a standing biomass of leaf litter 8.4% of healthy forest, although these differences were not tested statistically. Numbers of soil and litter invertebrates were generally lower in diseased forest, but there were variations between seasons and between taxa for both the soil and litter components. Nichols & Burrows (1985) recorded lower

numbers of invertebrate species and individuals in a diseased forest, as well as fewer trees and shrubs and lower mean litter cover values. Variations in abundance of invertebrate taxa were also observed between an uninfected forrest (*i.e.* n=1) and an infected (n=1) forest depending upon the habitat requirements of each taxon. For example, Dermaptera which require dense litter cover were only recorded in healthy forest, whereas the majority of ant species were found in both diseased and healthy forests, although the total abundance of ants was lower in diseased forest. The low number of sites in these studies makes statistically-testable conclusions impossible.

Reptiles and frogs have been surveyed in both healthy and diseased jarrah forest. Diseased forest supported lower numbers of species and lower abundances than healthy forest (Nichols & Bamford 1985). Some species however, were more abundant in diseased forest (*e.g. Pogona minor* and *Cryptoblepharus plagiocephalus*), perhaps reflecting the increased insolation on elevated surfaces (*e.g.* logs) which these species use for basking and foraging (Nichols & Bamford 1985; Wilson & Knowles 1988). Again, low site numbers precluded statistical testing of the data.

There is some evidence that there are differences in the avifauna present in diseased and uninfected forests. Nichols & Watkins (1984) described a dieback-affected forest that had low bird species richness and abundance compared with healthy sites. At another dieback site, however, the bird density and species richness were comparable to those in healthy forest. Some species were recorded in higher densities in diseased forest, while other species were absent, resulting in different bird species composition in the two forest types.

In a study of small mammal communities in heathy woodland and heathlands, Wilson (1990) and Wilson *et al.* (1990) found the percentage of vegetation modified by *P. cinnamomi* to be a significant variable in explaining small mammal diversity and density. Further studies by Newell & Wilson (1993) in heathy communities of the Brisbane Ranges National Park, Victoria, found the abundance of *Antechinus stuartii* to be lower in *P. cinnamomi* affected areas. Vegetation volume was significantly lower between 0 and 60 cm, in diseased areas and the abundance of *A. stuartii* was significantly correlated with this variable. The change in structure in diseased areas was predominantly related to the loss of the austral grass-tree (*Xanthorrhoea australis*). Whether this loss affected *A. stuartii* through reduced cover, or altered food availability was unclear. Studies in coastal heathland at Anglesea, in southern Victoria, found that several small mammal species *e.g. R. lutreolus* (swamp rat), *R. fuscipes* (bush rat), and *A. stuartii* (brown antechinus) were less abundant in diseased heathland than in healthy stands (Laidlaw & Wilson *unpublished data*). Mean species richness of small mammal communities was also lower at infected sites.

The utilization of habitat by the dasyurid marsupial *A. stuartii* in *P. cinnamomi* infected and non-infected areas have been investigated at several sites in the Brisbane Ranges, Victoria. *A. stuartii* was found to forage almost exclusively at ground level, and frequently used nest sites located at ground level in large *X. australis* plants (Newell 1994). The movement and home range of *A. stuartii* were investigated

using trapping and radiotelemetry. Home ranges displayed a high degree of overlap with areas that were uninfected with *P. cinnamomi* and animals actively selected uninfected habitat, and avoided areas infected with *P. cinnamomi* (Newell 1994). Individuals occasionally crossed bare, long-term infected areas to enter other uninfected habitat. These results suggest that *A. stuartii* relied heavily on vegetation cover. The effect of *P. cinnamomi* on the dietary items of *A. stuartii* was also investigated (Newell 1994). There was no relationship between invertebrate abundance, and the capture rate of *A. stuartii* in infected or unitected areas.

The above studies provide evidence that the modification of habitat due to the presence of *P. cinnamomi* can lead to declines in the overall abundance of fauna. There is evidence that these changes also result in reduction in species richness, and/or diversity. Changes in the abundance of individual taxa, may depend on their habitat requirements, with some taxa increasing and others declining. Some of the studies outlined were limited in design, and mainly addressed other environmental disturbances such as mining. There is evidence of altered utilization of habitat by *A. stuartii* due to the presence of *P. cinnamomi*. Further work needs to be undertaken to establish the relationships between the modification of habitat components and changes in faunal communities due to the affects of *P. cinnamomi*.

P. cinnamomi, disturbance and resilience

Australian vegetation and fauna communities are well adapted to disturbance factors such as fire. In areas where fire frequency is high, communities often exhibit high degrees of resilience (or more specifically, elasticity; *sensu* Waltman 1986) following disturbance. This resilience is likely to be a consequence of the evolution of adaptive features over long periods of exposure to disturbance regimes. The presence of *P. cinnamomi* may also be considered a component of a disturbance regime. However, there is evidence that *P. cinnamomi* has recently been introduced to Australia (Weste & Marks 1974, 1987) and native plant and animal communities have not been exposed to the regime for a long period of (evolutionary) time. Therefore these communities are unlikely to have adapted to the presence of *P. cinnamomi*.

Compared with the relatively ephemeral effects of fire, *P. cinnamomi* may have a severe and long-lasting impact on plant and animal communities. Infection generally results in removal of a wide range of susceptible species and leads to simplification of the understorey. Furthermore, the pathogen is capable of remaining in the soil following infection, so may reinfect vegetation or infect new vegetation. Secondary plant succession after fire normally results in the re-establishment of the original floristic community, following an initial floristic composition model (Noble & Slayter 1981). There is evidence, however, that susceptible plant species rarely recolonise after *P. cinnamomi* infection (Weste & Marks 1987). The only evidence of recolonisation is where the austral grass-tree (*Xanthorrhoea australis*) has been recorded, at least 20 years after infection (Dawson *et al.* 1985, Weste 1993). Given large alterations to vegetation species composition after *P. cinnamomi* infestation, it is difficult to predict regeneration of the original vegetation community (Grubb & Hopkins 1986).

There is often substantial recolonisation by small mammals after fire (Fox 1982; Fox & McKay 1981, Newsome *et al.* 1975, Wilson *et al.* 1990). Recolonisation rates depend on factors such as the fire regime, the regeneration of vegetation and sources of recolonisers (*i.e.* unburnt patches). Some species enter the succession early (2-4 years) due to their preference for diverse young vegetation, while others may take up to ten years to return (Fox 1982, Wilson *et al.* 1990). Successional changes of vegetation communities following *P. cinnamomi* infestation are yet to be established. The resultant community is likely to differ substantially from the original vegetation community. It is presently difficult to accurately determine animal succession patterns; however, one would expect a very slow recolonisation process resulting in a different faunal community.

Conclusions

It is clear from the above review that *P. cinnamomi* has the potential to severely influence the abundance and composition of many faunal commuities. These effects are largely indirect, resulting from changes in plant species richness and composition, and from alterations to the structural components of the habitat. Although data are limited, there is evidence that a broad range of taxa are affected including small mammals, reptiles, birds and invertebrates. The effect on individual taxa will depend on that species' requirements for food and shelter, and its reproductive and foraging strategies. It may be predicted that some generalist species which require relatively open habitats may be favoured, while more specialized species (especially those with restricted diets which inhabit dense species-rich shrublands) would markedly decline in the dieback-affected areas. Similar principles have been shown to apply in assessing the impact of fire on small vertebrates (Friend 1993), and open the way for predictive modelling of the impact of plant diseases on faunal populations.

In tandem with these broad approaches to develop a classification of tolerant and sensitive faunal species (as has been done for many plant species; Wills 1993), there needs to be more detailed studies of movement patterns and resource utilization for the most sensitive species, particularly those which are regarded as rare or endangered. Although detailed habitat utilization work has been carried out on *A. stuartii* in relation to infection by *P. cinnamomi* (Newell 1994), there has been little such work on other potentially sensitive species like *T. rostratus*, *P. apicalis* and the western pygmy possum (*Cercartetus concinnus*).

Unique and threatened communities also need to be identified, and measures enforced to assure their long-term protection from plant diseases. Such work is now underway in Western Australia, where a GIS-based decision support system is being developed to monitor and manage *Phytophthora*-sensitive taxa and communities, and experiments are being carried out to evaluate the efficacy of aerial application of phosphonate to control *Phytophthora* in native plant communities. It is only through application of such multidisciplinary studies that we can begin to understand the processes by which plant diseases influence the structure and composition of plant and animal communities.

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Disease and forest production in Western Australia with particular reference to the effects of *Phytophthora cinnamomi*

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Abstract

The native forests of Western Australia are valuable for production of timber and water, and for conservation and recreation. Plant diseases affect all of these values. Timber production is reduced and the aesthetic experience of the forest changed when trees are killed or lose vigour. Conservation values are affected when species are eliminated locally or forest structures are changed. The main forest diseases recognised in Western Australia are caused by fungi. They are dieback caused by *Phytophthora cinnamomi*, straw rots (*Armillaria luteobubalina*) and karri brown wood (associated with a variety of fungi).

The effect of one of these diseases, jarrah dieback, on forest production was examined in a five year dendrometer study of tree growth. Overall diameter increment of jarrah on dieback-affected sites was less than on either control or thinned but dieback-free sites. Growth rates varied greatly both between sites and between trees on the same sites irrespective of disease status. As a consequence, the effects of dieback on tree growth are difficult to separate from site factors (*e.g.* rainfall, soil, topographical position) and tree factors (*e.g.* genetic potential, age, vigour and dominance class).

Introduction

The native forests and woodlands are a major asset of Western Australia. State forests are the source of nearly 2 million cubic metres of timber products annually (Table 1), of approximately half the water used by cities and for irrigation in the south-west (total storage capacity 9 10⁵ megalitres, Olsen & Skitmore 1991) and provide a varied environment for tourism, recreation and education. Conservation values of the forests are also high as, even in areas subject to logging, disturbance has been much less intense than in neighbouring agricultural or urban areas (Havel 1989).

Table 1

Timber production in Western Australia in 1992/93 (from Conservation and Land Management 1993).

Category	Volume (m³)
Eucalyptus marginata (jarrah)	385 819
Eucalyptus calophylla (marri)	45 587
Eucalyptus diversicolor (karri)	195 613
Pinus spp. (mainly *Pinus radiata*)	149 487
Non-sawlog (*e.g.* chiplogs, firewood)	1 100 077

Diseases affect forest values adversely by affecting growth, hydrological cycles, stand structure and species composi-

tion. The major disease problem of Western Australia's native forests is dieback associated with the soil-borne fungus *Phytophthora cinnamomi*. The disease is often termed "jarrah dieback" because of its highly visible effects on this dominant forest species. Affected jarrah typically dies after one or more cycles of crown death alternating with periods of partial recovery. Other significant forest diseases identified in Western Australia are root rots and basal cankers caused by the fungus *Armillaria luteobubalina*, and brown wood and rots of karri associated with a number of fungi.

Armillaria luteobubalina occurs throughout the south-west forests (Pearce *et al.* 1986, Shearer 1992, Shearer & Tippett 1988). Although *Armillaria luteobubalina* is capable of infecting a wide range of hosts including jarrah, marri, karri, wandoo and *Banksia grandis*, it seldom causes deaths of more than individual trees or small patches of trees. *Armillaria luteobubalina* lesions are usually contained by periderms if the host is a vigorous mature tree. However, mortalities can occur when lesions cannot be contained or large numbers of infections are initiated. Trees of highly susceptible species (*e.g. Eucalyptus wandoo*) or which are small, whose vigour has been reduced by intense competition or drought, or are close to *A. luteobubalina*-colonised stumps supporting high local inoculum populations, are at the greatest risk of damage.

Brown wood of karri is a discolouration associated with infection by a number of fungi with *Stereum hirsutem* and *Hymenochaete* sp. being the most common (Davison & Tay 1991). Brown wood does not affect timber strength (Siemon, CALM, Perth, *pers. comm.*) but it is unsightly and has been identified as a precursor to rots (Davison & Tay 1991). Such rots are unlikely to develop in timber which has been dried to less than 20% moisture content (Bootle 1983). The extent of the brown wood problem in karri is difficult to assess as the discolouration is visible only when stems are sectioned.

However, a limited study of regrowth karri mainly from the Treen Brook area found brown wood in 73% of 270 trees sampled (Davison & Tay 1991). The generality of this finding is untested.

The effects of *A. luteobubalina* and karri brown wood on forest values and forest production are less well understood than are the effects of *P. cinnamomi*. More extensive reviews of current knowledge of the occurrence and biology of *P. cinnamomi*, *A. luteobubalina*, brown wood and other fungal pathogens and saprophytes of the south west forests are given by Hilton *et al.* (1989) and Shearer (1992).

This paper will illustrate some of the difficulties of assessing the effect of pathogens on forest production by describing recent attempts to measure the effect of *P. cinnamomi* dieback on growth of jarrah.

Jarrah dieback

Phytophthora cinnamomi infestation of native forest causes changes in stand density and species composition (Davison & Shearer 1989) which affect non-timber values such as water yield (Schofield 1990), biodiversity, honey production and recreation. *Pinus radiata* on susceptible sites can also be killed or damaged (Chevis & Stukely 1982, Butcher *et al.* 1983).

Phytophthora cinnamomi dieback affects an estimated 14.2% of the jarrah forest (32 000 ha of the 225 000 ha of jarrah forest mapped by aerial photography; H Campbell, cited by Davison & Shearer 1989). The northern and western parts of the jarrah forest are affected more than the southern areas (Batini & Hopkins 1972) possibly because of differences in climate and soils which affect fungal behaviour and in the intensity of human activities which spread the fungus (Shearer 1992).

Initial prognoses for the survival of the jarrah forest were pessimistic because of early experiences of rapid death of virtually all jarrah trees over large areas. Accordingly, much early work was directed to replacing the native jarrah with *Phytophthora* resistant exotic species (Bartle & Shea 1978). Better understanding of the factors affecting the spread of *P. cinnamomi* in the forest and of jarrah's ability to resist *P. cinnamomi* (see Shearer & Tippett 1989) coupled with changing community attitudes to forest management has resulted in a more optimistic outlook. Management policy now emphasises maintaining as much of the jarrah forest as possible and limiting the spread of *P. cinnamomi* to uninfected forest by controlling access (Conservation and Land Management 1987, 1989).

Quantifying the effect of dieback on forest production has been difficult. Estimates of the loss of diameter increment of jarrah due to dieback vary from an 87% reduction (Podger 1972), through a smaller 12% loss (Crombie & Tippett 1990) to no effect or even a slight increase (Davison & Tay 1988). It is probable that the outcome depends on the balance between the level of damage caused by the pathogen and the benefits of reduced competition as susceptible neighbouring trees and understorey plants are killed.

Methods

Nine sites comprising a dieback-affected and an adjacent dieback-free area were chosen in the jarrah forest between Perth and Dwellingup. The association of *P. cinnamomi* with the observed dieback symptoms was confirmed by recovery of *Phytophthora* from the dieback-affected areas at all sites. A further five dieback-free sites were included to extend the range of site occupation on dieback free sites to encompass that of the dieback sites. Sites selected included elements of the S site type of Havel (1975) as this is representative of the main area available for logging in the northern part of the jarrah forest. The dieback-affected sites and their characteristics are listed in Table 2. Four sites (Angle Swamp, Boundary Road, Canning Dam Road and Karragullen) were those for which initial results have been discussed by Crombie & Tippett (1990).

A low intensity fire affected the dieback-affected part only of the Ashendon Road site in the autumn of 1990. Such fires have been associated with increased growth rates (Davison & Tay 1988, Kimber 1978) but the effect in this instance in unknown.

Dominant or co-dominant trees of as nearly similar diameter as could be managed were selected on each of the dieback-affected and dieback-free plots. Selected trees were fitted with stainless steel dendrometer bands (Liming 1957) and increments recorded monthly.

Results

Mortality

Growth of jarrah on dieback sites was monitored for three to five years giving a total of 548 tree-years (number of trees x number of years). Eight trees on three sites died during this time (1.5 % per annum). This compares with previous re-
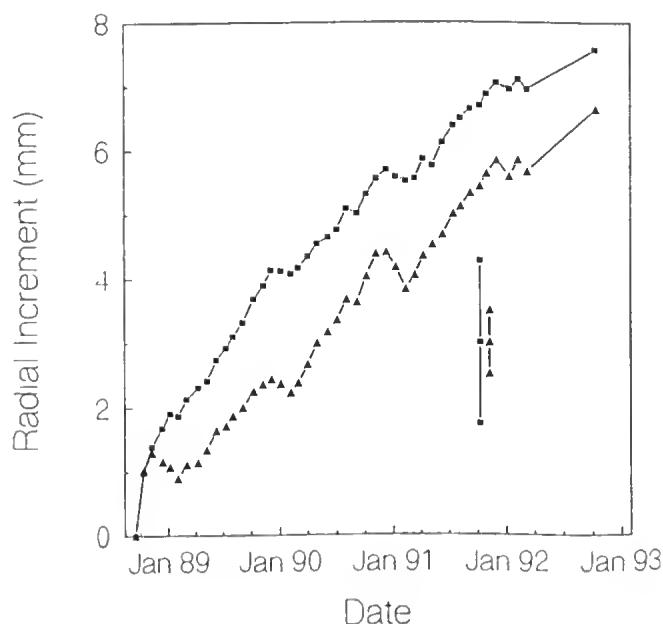
Figure 1. Radial increment of trees on adjacent dieback-free and dieback-affected areas at Pumping Station Road. Standard errors of increments between September 1988 and October 1991 are included (vertical bars) to show variability. There were 11 trees on the dieback-free area (■) and 23 in the dieback-affected area (▲).

Table 2

Characterisations of stands: C = Control, D=Dieback-affected, T=Thinned. Soil type; L=lateritic boulders and lateritic gravel, S-L=sandy soil with occasional lateritic rocks, S=sandy soil without lateritic boulders.

	Soil Type	Rainfall (mm)	Number of Trees		Diameter under bark (mm)		Height (m)		Stand Density (Stems ha⁻¹)		Basal Area (m² ha⁻¹)	
Dieback Sites			C	D	C	D	C	D	C	D	C	D
Angle Swamp	L	850	10	10	247	275	14	14	789	280	27	21
Ashendon Road	L	1050	12	12	330	323	18	18	1 353	1 626	31	29
Boundary Road	S-L	1050	11	11	226	251	18	19	865	654	28	22
Canning Dam Road	L	1250	10	11	282	265	19	19	1 054	318	31	24
Hay Creek	S	1100	11	11	326	306	17	15	926	912	34	32
Gravel Pit	S	1250	11	11	376	355	19	20	1 050	556	38	30
Karragullen	L	1250	10	7	252	255	16	16	1 455	919	31	24
Pumping Station Road	S	1200	12	21	303	248	18	15	934	458	34	20
Sawyers Valley	S-L	900	12	11	261	265	17	14	690	269	22	16
Thinned Sites			C	T	C	T	C	T	C	T	C	T
Banksiadale Road	L	1300	20	19	337	349	23	25	988	638	35	15
Jarrahdale Road	S-L	1200	12		314		24		1 549		44	
Mundaring	S-L	1100	40	60	251	246	17	17	1 498	1 472	29	21
Roma Road	L	1250	20	20	295	301	23	22	1 722	296	30	13
Torrens Road	L	1300	20	20	282	287	21	20	1 348	914	36	10

ports of report of 4.2 % per annum deaths (three sites, Podger 1972) and 0.84 % deaths per annum (two sites, Davison & Tay 1988). No trees died on dieback-free sites during this study. Deaths were unevenly distributed between seasons and also between years. Five deaths occurred when evaporative demand was high in mid to late summer (February to April) and three when it was rising in spring (September or October). More deaths occurred in 1991 and 1992 than in 1988, 1989 or 1990.

Growth

Radial increment varied between dieback-affected and dieback-free sites and also between trees within sites, between sites and from month to month and year to year. Typical growth patterns are illustrated with data from the Pumping Station Road site in Figure 1.

Stem growth occurred when soil water was readily available (from the beginning of rains in April or May until January or February) but was slowed by low temperatures during winter (June to August; see also Abbott & Loneragan 1983). Slower diameter growth or slight shrinkage were associated with water deficits during summer drought (February to March).

Growth patterns of trees on dieback-affected areas were similar to those of trees on dieback-free sites with the exception that summer shrinkage began one to two months earlier and was more pronounced in trees on dieback-affected sites. The effect of dieback on growth was examined by analysis of covariance using the total radial increment occurring be-

tween October 1988 and October 1991 (Table 3). Data were transformed to square roots to reduce heteroscedascity. Stand basal area (SBA) and site were identified as the major covariates by step-wise regression.

Table 3

Analysis of covariance. Tests were conducted by applying the SAS procedure General Linear Models to square root transformed radial increments from October 1988 to October 1991. SBA= Stand Basal Area.

Source	DF	Sum of Squares	Mean Square	F Value	P
SBA	1	13.83	13.83	21.12	0.002
Site	13	26.88	2.07	3.16	0.05
Dieback	1	1.93	1.93	2.94	0.12
Site* Dieback	8	5.24	0.65	1.93	0.05
Within plot	411	139.52	0.34		
Total	434	201.13			

Phytophthora cinnamomi dieback was less a predictor of tree growth (p = 0.12) than either stand basal area (p = 0.002) or site (p = 0.05). The low level of significance in the results reflects the small sample sizes used (10 to 12 trees per site). A *post hoc* consideration of the variances in growth suggests that a sample size of 30 trees would have been needed to obtain differences between growth of trees on dieback-affected and dieback-free sites significant at the 5% level.

Comparison of the adjusted mean squares solutions to the model (Table 4) shows that increment on dieback sites

averaged about 80% that on dieback-free sites. However, growth of trees on the dieback-affected areas relative to dieback-free areas varied widely from a minimum of 38% on the Angle Swamp site to a maximum of 140% at Ashendon Road.

Table 4
Mean of measured radial increments and least squares adjusted mean increments (as square root of increment) on dieback-free control (C) or dieback-affected (D) sites. Covariates used in the adjustment were stand basal area and site.

| Site | Radial Increment ($\sqrt{}$mm) | | | | Ratio |
| | Measured | | Least squares estimate | | (D/C) |
	C	D	C	D	
Angle Swamp	2.1	1.4	2.1	1.3	0.62
Ashendon Road	1.6	1.8	1.6	1.9	1.16
Boundary Road	1.9	2.1	2.0	1.9	0.97
Canning Dam Road	2.6	2.4	2.7	2.2	0.83
Hay Creek	2.2	1.7	2.3	1.8	0.78
Gravel Pit	2.1	2.3	2.3	2.3	1.01
Karragullen	2.7	2.9	2.7	2.7	1.02
Pumping Station Road	2.4	2.1	2.4	2.0	0.83
Sawyers Valley	1.8	2.1	1.8	1.8	1.03

Growth of trees on dieback sites was not affected in a consistent way by outcroppings of lateritic ironstone or sandy soils which might indicate differences in drainage. Thus while growth at two sites with masses of exposed lateritic duricrust (Angle Swamp and Canning Dam Road) was reduced below those of controls, growth was about the same at another site (Karragullen) and was increased substantially at a fourth (Ashendon Road). Of the sites with sandy soils, growth was reduced on the dieback areas at two sites (Pumping Station Road and Hay Creek) but was virtually unaffected on another two sites (Boundary Road and Gravel Pit).

Discussion

Synchronisation of tree deaths with times of high or rising evaporative demand and higher death rates in years with unusually high rainfall has been noted before (Davison 1988, Fagg *et al*. 1986, Shea *et al*. 1983, Hamilton, 1951 *unpub. report* cited by Dell & Malajzuk 1989, Tippett *et al*. 1985). Both observations are consistent with the expected behaviour of *P. cinnamomi* which requires water for dissemination and infection and which damages the roots necessary for uptake of water during summer drought (Crombie & Tippett 1990).

Overall radial increment of trees on dieback-affected sites was about 80% that of similar trees on nearby dieback-free sites, although the estimates are imprecise (see above). The lack of precision is disappointing given that the biotic and environmental factors affecting *P. cinnamomi* are well known (*e.g.* Shearer & Tippett 1989).

The greatest difficulty encountered was the great variability in tree vigour, age, size, spacing, genotype, topography and soil type which occur in native forests (Stoneman *et*

al. 1989). Determination of the effects of disease on growth of jarrah are made more difficult by the very slow growth of jarrah in native forest (diameter increments of 2-3 mm yr^{-1}) which require long periods before the effects of disease on growth become evident.

Locating suitable control plots was also a problem. Potential control sites adjacent to diseased areas are often disease-free because they have some characteristic which has prevented the pathogen occupying the site. Differences in soil type, amount of deep drainage and sub-surface topography may be very important in determining disease occurrence but are difficult to identify in the field.

Even when the factors controlling disease occurrence are known, other factors limit site selection. In particular, the location, shape and size of dieback outbreaks is largely dependent on the interaction of site hydrologic characteristics and forest operations. Dieback infestations originating from soil dropped from vehicles (Podger 1972) usually spread downhill along drainage lines leaving the tracks from which the infections began as the boundary between dieback-affected and dieback-free areas. Such tracks are often used as convenient boundaries for logging coupes or as firebreaks (as happened at the Ashendon Road site) so that stand structure and history are often not the same on both sides of the track. Areas downstream and possibly to the side of known infections must also be considered to be either infected or highly likely to become so as spores are distributed by mass flows of soil water (Kinal *et al*. 1993). Finally, plot access tracks have to be suitable for wet weather use without risking establishing new *P. cinnamomi* infestations.

The time since infection, occurrence of subsequent re-infections and the rate and extent at which dieback develops may also be important to the effect of dieback on growth but are seldom known when studying disease in native forests. Similarly, genotypic (Butcher *et al*. 1984) and environmental factors, including temperature and summer drought (Shearer & Tippett 1989, Tippett *et al*. 1987), are likely to affect the rate of development and severity of disease expression but cannot be controlled in most field situations.

Conclusion

This study has recorded both reductions and increases in growth of jarrah on *P. cinnamomi* infested sites. The provisional conclusion is that average diameter increments of trees on dieback sites are approximately 80% those on dieback-free sites when adjusted for differences in site quality and competition. Differences in the effect of *P. cinnamomi* on growth of particular jarrah trees are likely to be related to tree, site and climatic differences.

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The impact of plant disease on mining

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Abstract

Dieback disease caused by *Phytophthora* species is the only plant disease having a major impact on the bauxite mining operations of Alcoa of Australia Ltd and the mineral sands mining operations of RGC Mineral Sands Pty Ltd. To mine responsibly in regions of the state where dieback is a concern, both companies have implemented major dieback management programs. The financial costs associated with implementing these programs are substantial. However, estimating the total financial cost of dieback disease management on the mining operations is very difficult because dieback control procedures are integrated with mine planning and other operational procedures. Both companies recognise that these financial costs are part of the overall cost of mining in regions of Western Australia where dieback is present, and conservation of the natural vegetation communities is of high priority.

Financial considerations are not the only potential impacts of disease. Plant diseases can also impact on environmental management objectives. Dieback disease has the potential to affect three important environmental management objectives; protecting the adjacent natural vegetation, establishing key plant species in rehabilitated sites, and achieving high species richness in these sites. Achievement of these objectives is regarded as important to the success of the mining operations of both companies.

Alcoa and RGC monitor vegetation adjacent to their mining operations and rehabilitated areas for symptoms of dieback. There has been no *Phytophthora*-caused plant death found near RGC's operations in areas interpreted previously as uninfested. Monitoring of the forest surrounding a 120 ha bauxite mined area identified two new *P.cinnamomi* infestations; the total area was 0.32 ha. Establishment of key plant species in the rehabilitation (*Eucalyptus marginata* in the jarrah forest and *Banksia species* in the kwongan) has been successful despite the presence of *Phytophthora* species in the region. High species richness is achieved in the rehabilitated areas of both operations. Long term monitoring and continued research are still required on many aspects of this disease.

By developing dieback control procedures based on scientific knowledge of the pathogen and the disease process, and integrating these procedures with routine mining procedures, we believe both companies have successfully minimised the impact of their mining operations on surrounding and re-established native vegetation communities.

Introduction

Plant disease has a major financial impact on the mining operations of Alcoa of Australia Limited and RGC Mineral Sands Limited. However, there is more to impact than just financial considerations. Evaluation of the impact of disease on mining also needs to assess the impact of disease on the environmental management objectives of both companies. Achievement of these objectives is regarded as important to the overall success of the mining operations.

The only plant disease having a significant impact on Alcoa and RGC is dieback disease caused by *Phytophthora* species. This disease is a major threat to the native plant communities in the regions of Western Australia where both companies mine. Environmental management objectives have been developed for the mines; their focus is to protect the natural communities surrounding the mine and to create an ecosystem on the mined areas with vegetation similar to that which occurred before mining. The presence of dieback has the potential to prevent these objectives being achieved.

The aim of this review is to discuss both the financial impact of disease on Alcoa and RGC mining operations and the potential impact of plant disease on the environmental objectives of both companies.

Background to mining operations

Alcoa operates three bauxite mines in the jarrah forest, south east of Perth (Fig 1). Alcoa mines and rehabilitates an average of 450 ha of forest a year. Bauxite ore bodies tend to be on the mid to upper slopes and are of the order of 5-50 ha. The open cut mining procedures remove the hard laterite "caprock" and the more friable zone below the caprock. The depth of mining is usually between 3 and 5 m. Following mining the area is landscaped, the surface soil is returned and the area is ripped to remove compaction. Finally, the area is seeded with about 50 species of plants indigenous to
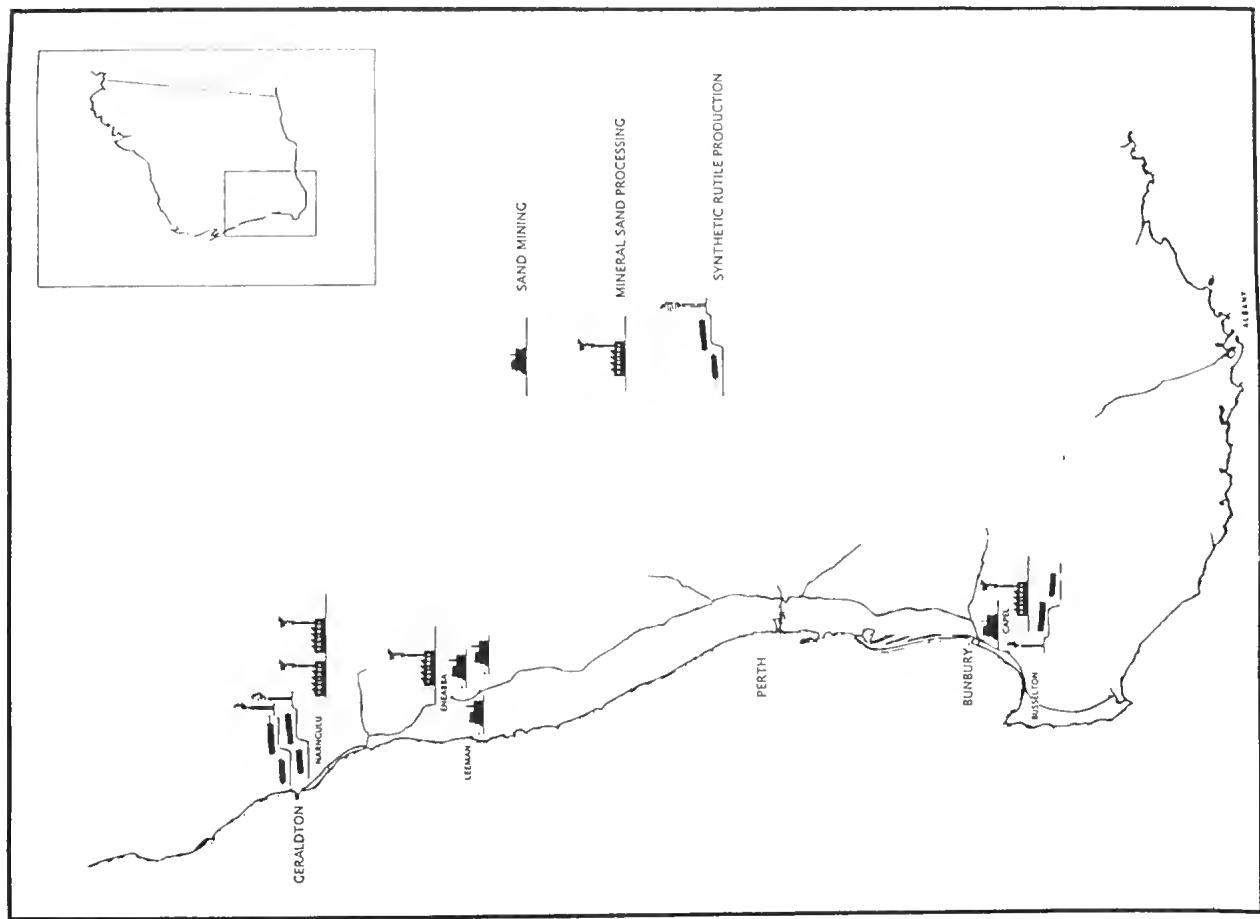
**Figure 2** Location of RGC's operations in Western Australia
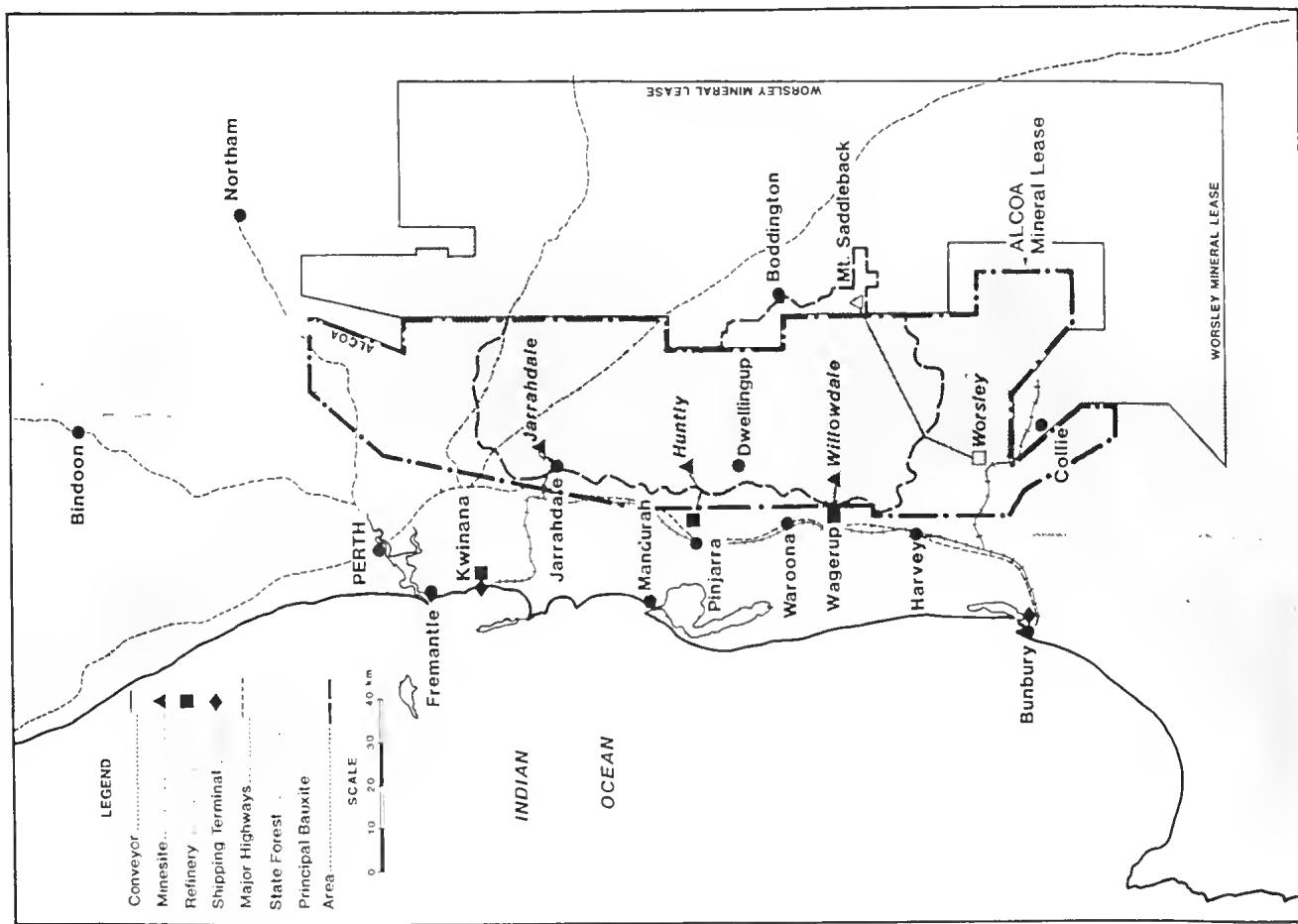
Figure 1 Location of Alcoa's operations in Western Australia

this region of the northern jarrah forest. Jarrah is established as the dominant tree species. The overall aim of revegetation is to create a community similar to the one present prior to mining. The mining and rehabilitation procedures are described in more detail by Nichols *et al.* (1985) and Ward *et al.* (1993). All mines are located in the western, high rainfall region of the jarrah forest where the extent of *P. cinnamomi* infestation is considerably greater than the estimate of 14% derived for the entire jarrah forest (Davison & Shearer 1989). *P. cinnamomi* infestation ranges from 66% of the forest at the Willowdale mine to 33% at the Huntly mine.

RGC mines and processes mineral sands to produce ilmenite, rutile and zircon. Its largest operations are near Eneabba on the Swan Coastal Plain about 300 km north of Perth and 30 km inland (Fig 2). Currently two mines are operating. One mine is a dredging operation whilst the second uses trucks, scrapers and other conventional dry mining equipment. The ore bodies are located underneath native heathland (kwongan) and agricultural land. The distribution of ore tends to follow long thin "strands" (*e.g.* 10 km long, 120m wide and 30m deep). Once the ore is mined, the heavy mineral is removed by wet gravity separation using water. The non-mineral slurry is pumped back to the mined-out pits where it is left to dry before it is landscaped, topsoil returned and revegetated. In the species-rich kwongan, the rehabilitation objective is to establish a self sustaining ecosystem similar to the undisturbed heath. Pre-mining surveys recorded 429 species from 50 families and 162 genera. Many of the principal genera are susceptible to *Phytophthora* species.

Plant diseases

Dieback disease caused by *Phytophthora* species is the only plant disease having a major impact on the mining operations of Alcoa and RGC. The term 'dieback disease' is used here exclusively to describe the diseases of native plants caused by *Phytophthora* spp, where infection leads to a 'root rot' or 'collar rot', and the eventual death of the plants. The earliest records for this disease in Western Australia came from the jarrah forest where there were unexplained deaths of jarrah trees in the early 1920s. The association between the deaths of jarrah and infection by *P. cinnamomi* was established in the mid 1960's (Podger *et al.* 1965, Podger 1972). Although this disease in the jarrah forest is commonly called 'jarrah dieback', it is known that many other species are susceptible to *P. cinnamomi* in a range of vegetation communities (Shearer & Tippett 1989, Shearer 1990).

Phytophthora cinnamomi is the most destructive of the seven species of *Phytophthora* found in south-western Australia. It is the only species having a significant impact on the mining operation of Alcoa (Colquhoun 1992) and it is the cause of most *Phytophthora* related deaths in the northern sandplain around the RGC mine. However, *P. citricola*, *P. megasperma* var *megasperma*, and *P. megasperma* var *sojae* are also known to have caused plant death in the northern sandplain (Hill 1990).

All of these *Phytophthora* species are soil borne and spread readily in soil and water. During mining, huge volumes of soil are transported, large road networks are established and the drainage of areas is altered markedly. All Western Australian mining companies working in *Phytophthora*-infested areas recognise that mining has the potential to spread the pathogens and thereby increase the area of infestation. The need for dieback control measures is also recognised by the companies. Alcoa and RGC have developed and deployed intensive dieback management programs to minimise the potential to spread the pathogens to native communities and rehabilitated mined areas. The dieback management programs are based on an understanding of the pathogen and the disease process. This understanding was gained from scientific studies; many of these were undertaken by local research institutions and funded by West Australian mining companies.

There is a range of other plant diseases which are having an impact on mining operations, but the impact is minor in comparison to dieback disease. A range of canker fungi have been isolated from plants growing in rehabilitated bauxite mined areas. The fungi identified include *Botryosporium* spp, *Botryosphaeria ribis*, *Cytospora eucalypticola* and *Pestalotiopsis* sp (Carswell 1993). Only on a few occasions has the presence of these fungi been linked to the death of a plant in the rehabilited areas. *Armillaria luteobubilina* is found frequently in the jarrah forest. Forest sites infested with this pathogen have been mined and the soil used in rehabilitation. Despite regular monitoring of deaths of plants in rehabilitation, and field reconnaissance of most rehabilitated pits, there has been no report of multiple deaths from this pathogen.

Alcoa and RGC operate nurseries which propagate native plants for use in the mine rehabilitation program. The control of plant diseases caused by species of *Phytophthora*, *Rhizoctonia*, and *Pythium* is critical to successfully producing container grown plants. Both Alcoa and RGC nurseries have been successfully accredited by the Nursery Industry Association of WA as meeting the required standards of *Phytophthora* disease control.

Two of the most important plant families in the Northern Sandplains are the Restionaceae (rushes) and Cyperaceae (sedges). Previous research had shown that most rush and sedge species in the Northern Sandplains are affected by smut diseases. These diseases may cause up to 100% reduction in seed set and reduce seed quality in many species. Smut-affected populations have been shown to have a significantly reduced capacity to recruit seedlings, particularly where the parent plants are killed by fire. Plants of a number of species become chlorotic and senesce following infection by smut diseases. Research work is currently being funded by RGC and conducted by Kings Park Board on controlling smut in rushes and sedges so that improvements can be made in their rehabilitation and the impact of these diseases is lessened.

The financial impact of dieback on mining

The dieback management programs of Alcoa and RGC are a major cost to the operations. Dieback control measures are present at virtually all stages of mining. Some major costs are easy to determine (Table 1) but the greatest will be the "hidden" costs associated with the day-to-day operations of the mines. Many stages of mining now take longer and require increased use of machinery. To minimise the disruptions to mining, the control measures have been integrated with the routine mine planning and operational procedures. Due to this integration the total financial impact is very difficult to determine.

Table 1
Major costs associated with Alcoa and RGC dieback management programs

	ALCOA $	RGC $
Construction of vehicle cleaning facilities	300,000	300,000
Dieback interpretation and mapping	200,000 per year	20,000 per year
Mapping site vegetation types	220,000 every 5 years	Not applicable
Dieback research funding of external projects	210,000 per year	10,000 per year

Rather than attempt to determine the cost of the dieback management programs for each company, we have provided an overview of the dieback management strategy used by RGC, and a comparison of one stage of bauxite mining with and without dieback control measures. These examples will demonstrate the complexity of dieback management and its associated costs.

Dieback management strategy - RGC

RGC has implemented a dieback management program that addresses hygiene practices, surveys, rehabilitation techniques, drainage patterns, education, research and regular reviews. Some key components of the strategy are:

- mapping the presence of dieback on and around the mining;
- advising all contractors, carriers and personnel of their obligations under the dieback management program;
- ensuring that all vehicles and equipment entering and leaving the site are clean of soil and plant material, by inspection and authorisation from suitably trained personnel;
- providing appropriate washdown and inspection facilities;
- constructing new roads and upgrading existing roads to dieback control standards *e.g.* developing a hard road surface and constructing roads above ground level;
- liaising with the Department of Conservation and Land Management, land owners and other authorities to control unauthorised access;
- developing procedures for movement of vehicles and equipment between sites and locations;
- segregating soil from dieback and non-dieback areas; and
- supporting research to increase the understanding of the disease and to develop improved dieback control measures.

Alcoa employs a similar dieback management strategy. As part of this strategy, Alcoa has developed detailed dieback control measures for each stage of mining.

Dieback control measures associated with overburden* removal and storage - Alcoa

During this phase of bauxite mining, all of the overburden is stripped from the orebody (using scrapers) and stored in large stockpiles. Following mining and landscaping of the minepit this overburden is returned to the area. Without dieback control measures, the process is simple; the scraper traverses the orebody in the most efficient manner to remove the overburden and transports it to a stockpile. The stockpile is usually located at the edge of the orebody, in the most convenient position for the operations (Fig 3a).

With the application of the current dieback control measures for stripping overburden at the Huntly mine, the operating procedures now involve (see Fig 3b):

- mapping for the presence of dieback (approx. 10,000 ha for 10 years of mining at one mine);
- marking the dieback boundary in the field. This boundary tends to split the orebody into "dieback" and "dieback-free" areas;
- surveying the boundary lines and recording these on a geographical information system (GIS) for use by mining and environmental planners;
- stripping the "dieback" and "dieback-free" overburden separately;
- ensuring that all vehicles moving across the dieback boundary into the "dieback-free" area are free of infested soil. Vehicle cleaning stations are located on the boundaries;
- storing the "dieback" and "dieback-free" overburden in separate stockpiles;
- selecting stockpile locations where the risk of spreading *P. cinnamomi* and the risk of increasing the impact of the pathogen in the infested forest is minimal. This generally results in the "dieback-tree" stockpiles being constructed in a previously mined area, where the risk of water draining from the stockpile into the uninfested forest is prevented, and
- where necessary, increasing the vertical infiltration of water of the site selected for the stockpile. This usually involves blasting the rock layer on and downslope of the future stockpile area.

The impacts of dieback control procedures on the day to day operations of removing and storing overburden are manifest; the procedure takes longer, requires more environmental monitoring, requires more resources (scrapers, drill rigs from blasting, surveyors, GIS operators, *etc.*) and requires more education and training of the operators and planners. This level of intensity of dieback control is achieved at all stages of bauxite mining and rehabilitation.

To collate the "hidden" costs associated with dieback management for RGC and Alcoa would be a complex and arduous task, and we do not believe that this is necessary. Both companies recognise that these financial costs are part of the overall cost of mining in the region of Western Australia where *P. cinnamomi* is present and the conservation of the natural vegetation communities is of high priority. How-

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* Overburden is the part off the soil profile above the ore layer, which remains after the topsoil (top 15 cm of the profile) has been removed. The nutrient level and seed load is low in the overburden so this soil is stockpiled and returned during the rehabilitation phase.
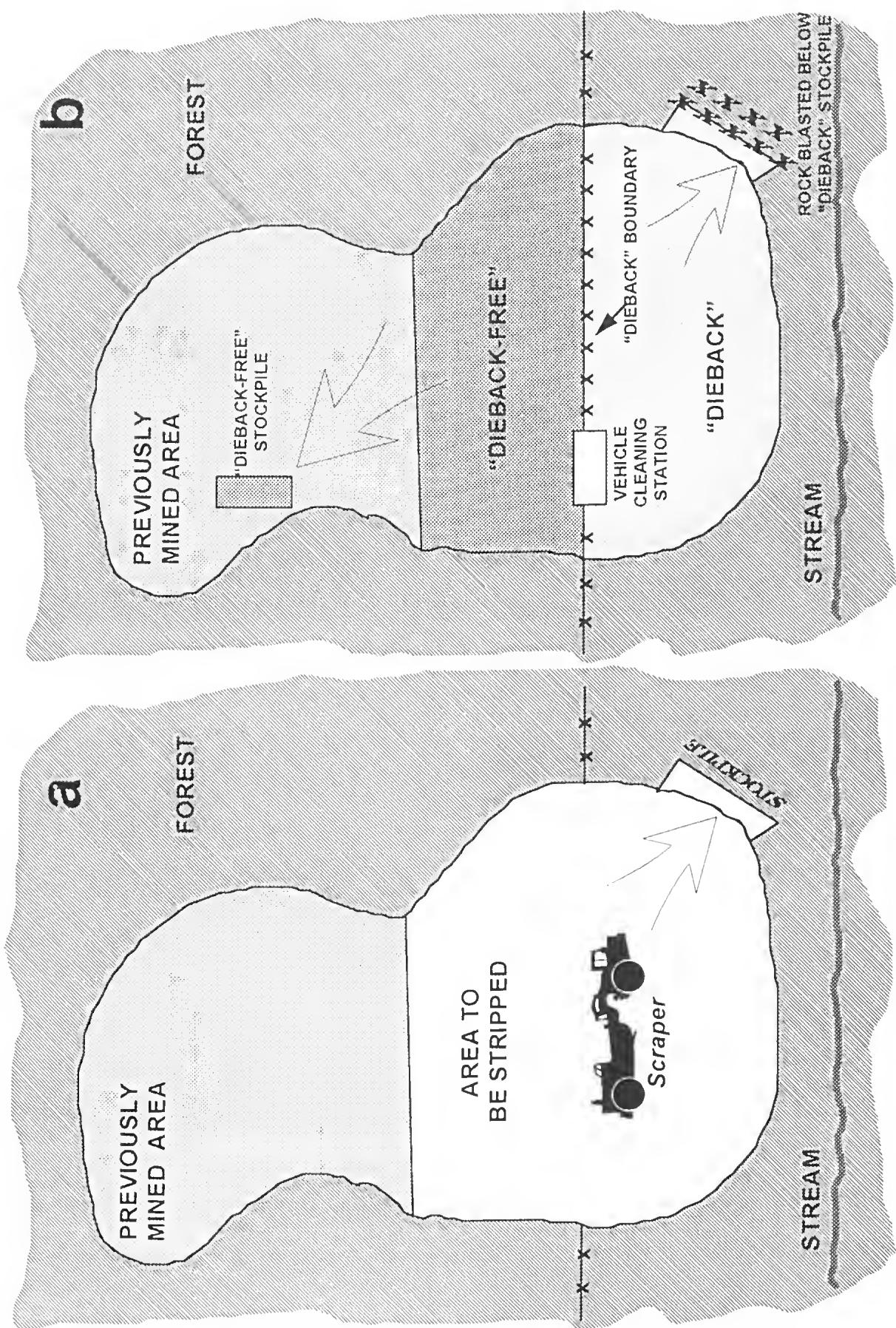
Figure 3. Schematic of the operation of stripping overburden from a bauxite ore body, (a) without dieback control measures and (b) with dieback control measures.

ever, research and development work continually aims to develop more effective and less expensive procedures.

Impact of dieback on environmental objectives

Dieback has the potential to adversely affect three important objectives for the environmental management of the mining leases:

- protect the vegetation surrounding the mined areas,
- establish key plant species in rehabilitated mined areas, and
- achieve high species richness in rehabilitated mined areas.

Protection of the adjacent natural vegetation

This environmental management objective is to prevent mining from causing significant adverse effects on natural communities near the mines. The spread of *Phytophthora* species to these sites has the potential to have a major impact on the health and species composition of these areas. Consequently, a critical aim of all dieback management programs is to prevent the spread of the pathogen to uninfested, natural communities. Control measures are introduced to minimise the risk of infested soil or water being deposited in these areas.

At Alcoa, attempts are being made to quantify the level of spread of *P. cinnamomi* that can be directly related to mining operations. The procedure involves identifying pits where the adjacent forest was uninfested before mining then re-mapping for dieback symptoms after rehabilitation. The increase in the area of infested forest is then calculated. Any new infections found abutting the pit edge would, in most instances, be attributed to mining. This procedure has been applied to an area at the Huntly mine that received the current intensive dieback control measures. This large mine pit was mined from 1986 to 1990 and rehabilitated in 1991 and 1992. The total area mined was 120 ha and 13.5 km of the pit edge abutted forest interpreted as "dieback free" before mining. The re-interpretation of the pit edge in 1993 identified two new infections; the total area of the new infections was 0.32 ha. This is 0.23% of the area cleared for mining.

Monitoring of the spread of the pathogen provides information on the impact of mining on the adjacent community; it also provides vital feedback on where and how the pathogen is being spread. This feedback is used to improve the dieback control procedures and their implementation.

At RGC the natural vegetation communities around the orebody are inspected regularly. There has been no *Phytophthora*-caused plant death found near the mining operations in communities previously interpreted as uninfected.

The protection of native communities is an important part of environmental management of most mining operations. The measured spread of *Phytophthora* species to these communities is very low but we believe that some long term monitoring is required to ensure that the companies' environmental objectives continue to be achieved.

Establishment of key plant species

The establishment of particular plant species is regarded as important to the success of mine rehabilitation in the jarrah forest and kwongan. In the jarrah forest the key species is jarrah and in the kwongan the dominant *Banksia* species are regarded as key species. All of these key species are susceptible to *Phytophthora* species

Alcoa and RGC mine *Phytophthora*-infested areas so, irrespective of dieback management programs, *Phytophthora* species will be present in some of the rehabilitated areas. Will the presence of *Phytophthora* species prevent the establishment of these key species?

The objective of re-establishing a forest dominated by jarrah after bauxite mining was not considered in the early years of mining. It was assumed that the presence of *P. cinnamomi* would kill the trees. However, in 1978 and 1979 jarrah was established at two mines. In 1986, trials were established at all mines to assess the establishment of jarrah from broadcast seeding. The success of this trial, and high survival of jarrah trees established in earlier revegetation, led to jarrah being re-established as the dominant tree species in most rehabilitated sites after 1987, and all sites after 1991.

Phytophthora cinnamomi has been isolated from dead jarrah plants and soil in rehabilitated mined areas but survival of jarrah is high in both the infested and uninfested sites (Fig 4). The present target for jarrah establishment is 2000 trees ha^{-1} after 9 months. The eventual stocking density of these sites is expected to be similar to a fast growing regrowth forest site *i.e.* 300-500 trees ha^{-1}. In 1993 the mean stocking density of jarrah in 32 rehabilitated pits, 9 months after seeding, was 2790 trees ha^{-1}. Only two pits had less than 1500 trees ha^{-1}.

So despite the presence of *P. cinnamomi* in rehabilitated areas, the early stocking rates are high and the present rate of mortality of jarrah in the rehabilitated areas is low. A cooperative research program with CALM, Murdoch University and Edith Cowan University is identifying and propagating jarrah plants that are known to have a high resistance to *P. cinnamomi*. Another major research program has been initiated to gain a better understanding of the factors affecting the survival of jarrah in revegetated bauxite mined areas. These programs should lead to greater certainty on the long term survival of this key species.

At Eneabba, *Banksia hookerana*, *B. attenuata*, *B. leptophylla* and *B. candolleana* are propagated in the company nursery and planted into the rehabilitation. Successful rehabilitation has been achieved despite these species being very susceptible to *Phytophthora*. The banksia seedlings are not planted in high risk areas such as drainage lines. This mimics the natural situation where banksias are usually restricted to the dune ridges and slopes and are not found in seasonally wet depressions.

The results of the monitoring programs suggest that *Phytophthora* species are not having a major impact on the establishment of key plant species in the revegetated mineral sand and bauxite mined areas.
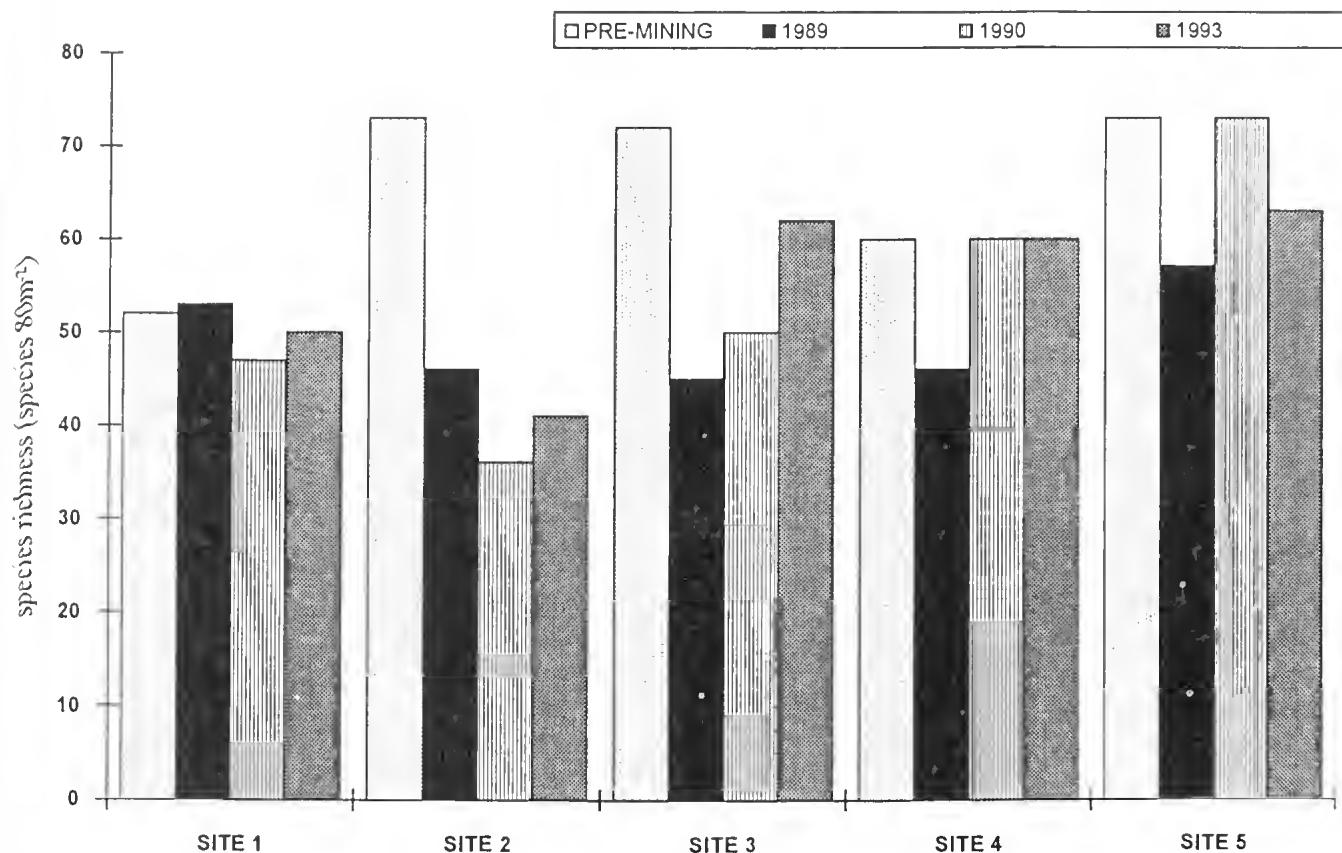
Figure 4. Species richness of five rehabilitated bauxite mined areas monitored one, two and five years after mining (Ward, *unpublished data*).
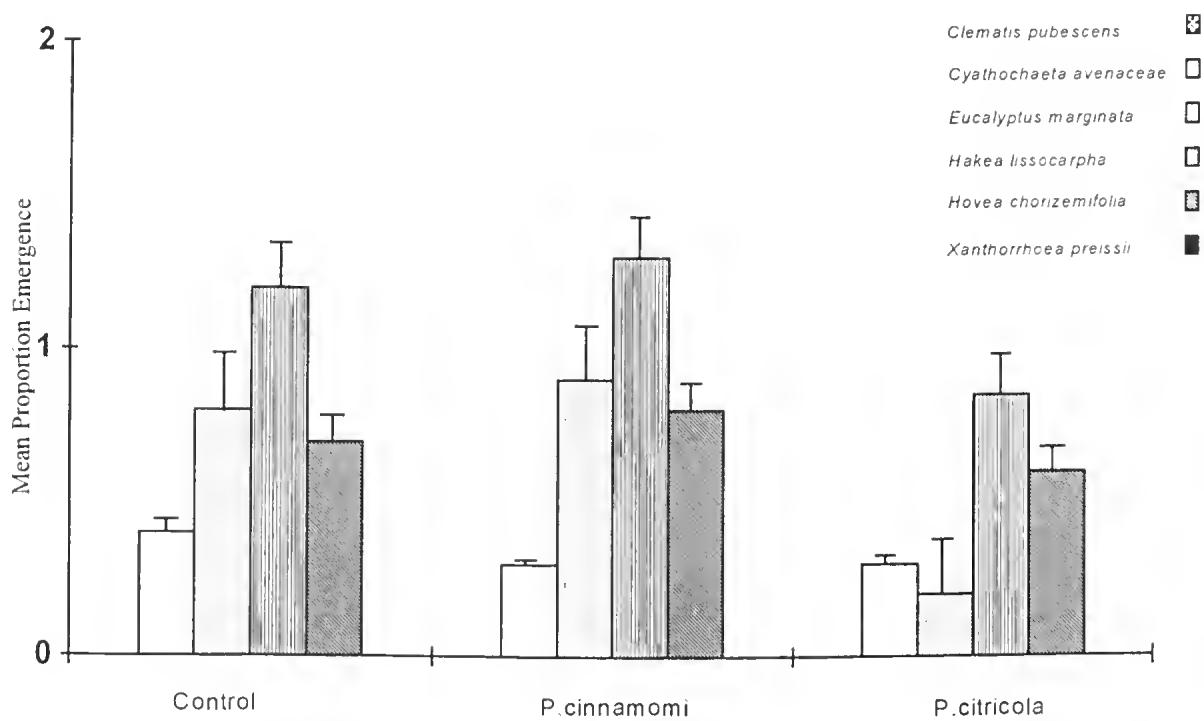

Figure 5. Mean proportion of seedling emergence of six species in a revegetated bauxite mined area monitored six weeks after seeding (from Woodman 1993). Emergence presented as least square means of arcsine transformed data with standard error bars. Seedlings *C. pubescens* and *X.preissii* were not found.
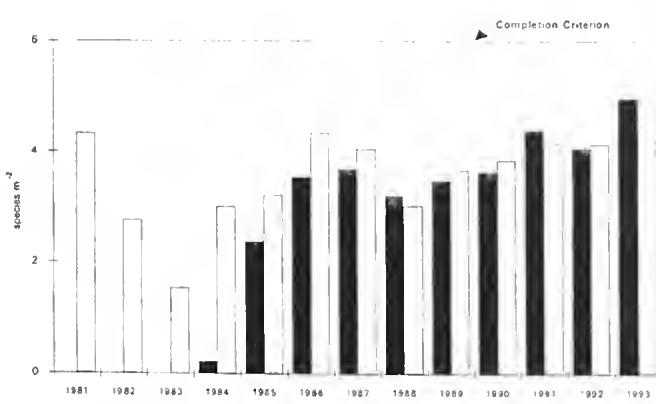
Figure 6. Mean species richness of rehabilitated mineral sands mining areas, one year after establishment and as monitored in 1993.

Establishment of high species richness

The objective of the present rehabilitation techniques for bauxite-mined areas is to establish a vegetation with a high species richness, similar to that of the adjacent forest. Some species are known to establish well from the seed present in the topsoil, other species establish from seed spread on the pits during rehabilitation. The impact of *Phytophthora* species on plant species richness is difficult to assess. Many factors affect plant establishment; plant disease is just one of many. Present levels of species richness in rehabilitated bauxite mined areas are high (Fig 5). Initiatives are underway at all mines and Alcoa's nursery to increase species richness. Very few deaths of susceptible species are found during inspections of rehabilitated areas. However, only the death of older plants, of easily observable size, would be found. *Phytophthora* species may kill the seed or the young (<6 weeks) seedlings of some species. Death at this stage would go unnoticed. Preliminary studies of six plant species found that *P. cinnamomi* had no significant (P=0.05) effect on the emergence of seedlings in two rehabilitated mined areas (Fig 6). However, *P. citricola* did significantly reduce the emergence of two species (Woodman 1993).

For RGC, the achievement of a high species richness (average of six plants per square metre) is a formal completion criterion for their revegetated mined area at Eneabba. Species richness is monitored every year. Results to date indicate that there is a consistent increase in species richness over time and that the revegetated areas are developing a richness comparable to the unmined vegetation (Fig 7). Therefore, the impact of *Phytophthora*, whilst it can be dramatic in isolated infections, does not appear to be limiting the overall success of the rehabilitation program at Eneabba.

More research and monitoring is required before the impact of *Phytophthora* species on the species richness of rehabilitated areas can be fully assessed. However, early indications are that high species richness can be obtained despite the presence of *Phytophthora* species.

Conclusion

Alcoa and RGC operate large mines in a region of Western Australia where the native vegetation is susceptible to disease caused by *Phytophthora* species. The challenge to both companies has been to develop and implement disease management programs which ensure that mining has minimal impact on the health of the native communities and the revegetated mined areas, while minimising the financial cost to the companies. The present financial cost of the programmes is significant but the results to date indicate that the disease management measures are successful. However, monitoring of their effectiveness needs to continue. Both companies accept that these costs are part of the essential costs of mining in these regions of the State, but research and development will continue to seek more cost effective disease control measures.

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Threats to flora-based industries in Western Australia from plant disease

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Abstract

The flora of south-west Western Australia is known internationally for its rich array of species and its uniqueness. This floral wealth attracts many visitors, supports a thriving export trade in cut flowers, and contributes to one of the highest rates of honey production in the world. Many of these plants also have outstanding value or potential for amenity horticulture and floriculture. More recently, the importance of bioresources was highlighted by the discovery of a chemical, derived from a species of *Conospermum*, capable of inhibiting Human Immunodeficiency Virus (HIV). The Proteaceae are a key element of south-western Australian ecosystems, and are a key resource of all of these industries. *Banksia* and *Dryandra* are of particular importance for their attractive blooms, and are heavily exploited for their inflorescences, foliage and seed, and offer an important source of nectar. The destruction of large stands of these disease-susceptible species by a combination of aerial canker and *Phytophthora* diseases, clearing, fire, and other disturbances could cause a significant financial loss to all flora-based industries. Notably, these flora resources are used with little return to the State for their conservation and management. An attempt is made here to quantify the financial impost of such losses, and a case is made for the need to invest in the protection of these bioresources through appropriate management.

Introduction

The ecological impact of plant pathogens has been well documented (see Shearer 1994 and Wills & Keighery 1994), but the economic implications for flora-based industries are poorly understood. The destruction of large stands of susceptible species by various diseases, particularly where other disturbances such as clearing, fire and weed invasion act in concert, could cause a significant financial loss to all industries reliant on the native flora. This brief review highlights some of the potential threats of plant disease to various flora-based industries, and focusses in particular on the family Proteaceae, a key element of south-western Australian ecosystems, often a key resource of these industries, and highly susceptible to dieback disease and aerial canker.

Wildflower industry

The wildflower industry in Western Australia employs about 150 people full-time, and up to a total of 200 people during spring and summer (Anon. 1992). The principal product is dried flowers, but fresh-picked flowers, seed, and resource for craft-based cottage industry (using flowers, nuts, seeds, and dead woods) are also significant. Western Australia dominates the Australian export market, providing the majority of overseas sales (Castles 1993).

In 1992/93, the wildflower industry in Western Australia earned about $17 million. Wildflower exports contributed most, earning about $12 million (57% of all Australian wild flower exports) with about $4 million of this generated from bush-picked flowers. Currently 29% of bush-picked production comes from private land and 71% from Crown Land (Anon. 1994).

The Proteaceae are an important resource for the wildflower industry. In 1982, five of the 10 most heavily exploited genera were of the family Proteaceae (Burgman & Hopper 1982). Species of *Banksia* and *Dryandra* made up 17% of the stems picked, with two species (*B. baxteri* and *B. grandis*) the most heavily exploited for foliage; *Banksia* spp. were also heavily exploited for seed, making up 16% of all seed harvested by weight and 23% by value.

The impacts of plant diseases on the wildflower industry have been greatest in the south of Western Australia, east of Albany. In that area, commercial harvesting is based heavily on *B. coccinea* and *B. baxteri*. Both of these species have been severely affected by the root rot *Phytophthora cinnamomi* and more recently aerial canker.

From the mid or late 1970's, the *B. coccinea* harvest was concentrated on unvested reserves at Gull Rock and Cheyne Beach (25 and 80 km east of Albany respectively); picking of *B. baxteri* was centred on Cheyne Beach. In 1980-81, these species contributed 516,500 and 212,133 flowering stems respectively, to the total of 13,814,000 in Western Australia (Burgman & Hopper 1982) with the majority of these (at least two thirds) picked from Crown land. However, by the late 1980's these areas had been degraded to such an extent, that they were closed to pickers by CALM and other agencies. The creation of illegal vehicle tracks throughout these once dense stands appears to have contributed to the introduction and spread of *P. cinnamomi*. The disease has spread rapidly through sites killing many susceptible species including

species of *Banksia*, and has resulted in major structural changes to the vegetation (see Wills & Keighery 1994).

As these areas were degraded, wildflower harvesting activities moved further east, concentrating on unvested reserves near Cape Riche. In assessing *B. coccinea* and *B. baxteri* across their natural ranges from around Albany and east to Esperance, Robinson (1991) found the remaining stands of both species were seriously threatened by aerial canker and *Phytophthora* dieback. The study highlighted that areas at Cape Riche, 100 km east of Albany, had numerous large *P. cinnamomi* infestations introduced as a result of the "bush bashing" of illegal tracks for wildflower picking. The study also noted that there had been a surge in picking activity on private land in the late 1980's as many farmers sought an alternative income by harvesting *B. baxteri* when returns from normal rural activities declined dramatically.

The combined impact of picking activities and plant disease depleting available stocks led to a ban on the picking of both species of *Banksia* from Crown land by the Minister for the Environment (*B. coccinea* in September 1991 and *B. baxteri* in March 1993), and has forced the supply of *B. coccinea* and *B. baxteri* from Crown land to private land. However, as many remnant stands of *Banksia* on private lands have also been destroyed by *Phytophthora* and aerial canker, there is now a strong move toward cultivation of both species.

The volume of trade in *B. baxteri* was 665,000 stems in 1991, largely through picking from private land (Robinson 1991). Similarly, 60% of 305,000 stems of *B. coccinea* produced in 1991 was derived from plantations (Robinson 1991). Notably, a recent study has suggested that remnant bush managed for sustainable harvest of wildflowers may, in particular areas, produce a return per hectare as good as that obtained by traditional forms of cropping (ACIL 1993).

In the long term, the cultivation of native flowers to supply the industry should ensure better quality (particularly through horticultural selection of preferred forms) and reliable supply. Although *Phytophthora* has been recorded within some cultivated stands around Albany for more than five years, its impact has not been as devastating as in natural bush. The disease can be controlled by application of the fungicide phosphonate ("phosphorous acid"; Shearer & Fairman 1991, Komorek *et al*. 1994, Hardy *et al*. 1994).

Aerial canker disease may prove to be a greater problem in plantations. Canker fungi may be spread by cross infection from secateur wound sites (J Bathgate, CALM, *pers comm*), and it has been shown that the frequency of infection was greater through wounded tissue (Bathgate *et al*. 1994), so it is possible that wildflower picking may accelerate the spread of aerial canker disease through *Banksia* stands. Fortunately, cross infection can be prevented or controlled by use of appropriate hygiene measures such as the application of fungicides on wounds and equipment.

Plant disease has also impacted on the native seed industry through the destruction of natural stands of *B. coccinea* by *P. cinnamomi*. Currently, stocks of seed of this species are very low and demands are not being met by traditional sources (P Luscombe, Nindethana Seeds, *pers comm*). South Australia is an alternative seed source, but the well established cut flower industry in that state is reluctant to supply

Western Australia. *B. coccinea* is now also being established commercially in south-eastern Victoria. Although the trend is toward cloning of superior forms, there will always be a demand for seed to explore the natural variation within the species.

Beekeeping

Reliance of apiculture on native floral resources is unique to Australia; in Western Australia the honey crop is gained almost entirely from native plant communities. Commercial apiarists in Western Australia practise migratory beekeeping utilising flowering of various *Eucalyptus* species in forests in the south-west of Western Australia in late spring, summer and autumn, and relocate to the sclerophyll shrublands of the Northern Sandplain for the winter flowering (Wills 1989). In contrast, beekeeping in the rest of the world generally relies on agricultural crops (mainly legumes) as their major source of pollen and nectar, and there is generally no winter production (Grout 1949, Nye 1980).

In 1992, Western Australia produced 2,264 tonnes of honey (Kelly 1993) worth about $2.25 million. While Western Australia is the second smallest producer, producing only 14% of the Australian honey crop, rates of production are the highest in Australia and among the highest in the world (Wills 1989).

Honey bees tend to favour species which are either widespread and/or locally abundant, although some abundant species may not be visited (van der Moezel *et al*. 1987, Wills 1989). On the Northern Sandplain, Wills (1989) found that 93% of the total 125 species visited by honey bees were native woody perennials. The same study found that virtually all species of *Hakea*, *Grevillea*, and *Banksia* (Proteaceae) were utilised by honey bees. Two species of Proteaceae, in particular *Dryandra sessilis* and *Hakea trifurcata*, are considered by beekeepers to be the most important species in the region.

Given that *P. cinnamomi* is principally a pathogen of woody perennial plant species, that most species of Proteaceae are known to be susceptible to dieback disease, and that the Proteaceae are a significant resource for honey bees, then this plant disease poses a very serious threat to apicultural resources, especially in the Northern Sandplain area. Loss of native floral resources through land clearing has been identified as one of the most important threats to the continued economic development of the honey industry (Anon. 1983, Anon. 1984, Blyth 1987). Indeed, that part of the honey industry reliant on available native floral resources may have already reached an upper limit (Anon. 1984); any loss of native vegetation as a result of land clearing, fire, disease and other environmental perturbations will inevitably lead to a decline in apicultural production.

Biodiversity industries

The Convention on Biological Diversity (established in Rio de Janeiro at the Earth Summit, 1992) included a resolution to ensure access to genetic resources for environmentally sound uses while affirming national sovereignty. The Convention highlights the increasing global awareness of the importance of genetic resources in the production of valuable pharmaceutical, industrial and agricultural products.

South-western Australia is home to about 9000 species of plants, and as many as 2000 species may be susceptible to *phytopthora* (Wills 1993). The Proteaceae are a key family in Western Australia with 618 species and subspecies, by far the greatest concentration in the world; many of these have outstanding value for amenity horticulture and floriculture (Lamont, Wills & Witkowski, *unpubl. obs.*), and most are susceptible to dieback disease.

One species of Proteaceae in the genus *Conospermum* is of particular significance in the area of therapeutic drugs. Extracts from this species have been found to contain chemicals that inhibit Human Immunodeficiency Virus (HIV) *in vitro*. In the spirit of the Biodiversity Treaty, the WA Government has negotiated an agreement with commercial interests which ensures proper protection of the plant and guarantees profits to the State if the chemical proves an effective treatment for HIV. The discovery has already earned the State $1.7 million, and if successfully developed for market could potentially earn royalties in the order of $100 million per annum (Armstrong & Hooper 1994, Armstrong & Abbott *pers. comm.*)

The Department of Conservation and Land Management is establishing bioprospecting based on four principles:

- the WA community receives an equitable share of commercial benefits derived from use of the State's biological resources;
- research and development of WA's biological resources shold involve WA's scientific community;
- development of biological resources must be sustainable; and
- WA's biological resources must be protected and conserved.

Tourism

Tourists undoubtedly select destinations for a host of reasons, making it difficult to determine the actual contribution of floral resources to earnings in the tourist industry. The total 1989/90 income derived from tourism in Western Australia was $2,785 million, estimated using the multiplier effect (Western Australian Tourist Commission 1991). In 1989/90 around 20% of tourist day-trip destinations involved a visit to a national park/reserve or a scenic drive (Western Australian Tourist Commission 1991). These activities involved some interaction with and appreciation of the natural features of the surrounding landscape and particularly the flora. Further, 11.5% of 33,246,700 visitor nights in 1991/92 resulted from trips to view wildflowers (Western Australian Tourist Commission 1992). This puts an upper range of the potential annual value of floral resources to the tourist industry of about $280 million to $560 million. The Western Australian Tourist Commission found that 116,000 group trips were specifically undertaken to view wildflowers, with visitor expenditure of about $36 million (A Sands, *pers comm*). Consequently, any factor, such as plant disease, which degrades this natural floral resource might be expected to have a substantial negative impact on the economy of Western Australia. Or will it?

The Albany area receives about 250,000 tourists per year (Western Australian Tourist Commission 1992); the Stirling Range National Park, famous within Australia for its wildflowers, received 209,000 visitors (tourists and locals) in

1992/3. Notably, the next most popular visitor destination in the Albany area with 180,000 visitors was The Gap, a natural rock feature above the ocean.

A popular destination for visitors to the Stirling Range is Bluff Knoll, which received 36,000 visitors in 1992/3, yet the flora of Bluff Knoll has been severely affected by the spread of *Phytophthora* dieback disease from the lower slopes right up to the summit plateau. The jarrah woodland on the lower slopes has been severely diseased and species such as the Giant *Andersonia* (*A. axilliflora*), *Dryandra montana ms* and *Banksia oreophila* have been killed on the plateau. *Banksia brownii* which was once common is now absent from the summit and upper slopes. The dieback resistant sedge, *Lepidosperma* sp. has become far more common and dominant in large areas over the past ten years as dieback has altered the vegetation structure (G J Keighery, CALM, *pers comm*, Keighery *et al.* 1993, see also Wills 1993). However it is apparent that most tourists visit only once and do not appreciate the presence of dieback in the landscape. Most are still delighted by the flora and do not notice dieback disease which is so apparent to the trained eye.

The 1992 Spring period (September - December inclusive) accounted for 66% of visitors to the Stirling Range; up to 90% of the patrons to Stirling Range Caravan Park come from the Eastern States to see the flowers of the Stirling Range (G Souness, Stirling Range Caravan Park, *pers comm*). However, other high periods of visitation simply coincide with school holidays (Conservation and Land Management 1992) in January (11%) and April (13%). Clearly, the flora is not the only attraction to the Stirling Range, perhaps not even the main attraction. Even so, publicity in eastern Australia or overseas of the impact of dieback on the flora could potentially have adverse effects on flora-based tourist interests in Western Australia.

Downline Effects

Decline in activity of any of these flora-based industries will have flow on effects to other service industries that cater for all of the above. Because operations using native floral resources are necessarily regionally-based, they can be quite significant in the economy of small towns, and this may in turn contribute immeasurably to social values by supporting associated community infrastructures.

Conclusions

Clearly, the destruction of large stands of these dieback-susceptible plant species by a combination of disease, clearing, fire, and other disturbances could cause a significant financial loss to all flora-based industries. Protection of bioresources through appropriate management is not only in the interest of conservation, but carries with it financial benefits of the existing resource as well as retention of bioresources of yet unknown value.

The wildflower industry may eventually be able to obtain most of its requirements from plantation; beekeeping might also be able to link into the expansion of plantations for both the wildflower industry and also for agroforestry. But, wildflower-based tourism and biodiversity-based industries will necessarily rely on a relatively pristine bushland for

their continuation, and wildlfower plantations will still require wild gene pools to maintain and extend varieties under cultivation.

Recommendations

Education of industry groups should be a part of licensing requirements for operation in wild populations of plants. All industries using natural bioresources tend to deny they are, or are ignorant of, contributing any significant ecological damage to the resource that sustains them. Managers and industry both agree that accurate statistical information provides a valuable resource for management; both groups must co-operate to ensure that information obtained as a part of licensing is both accurate and relevant, and that the results of its analysis are put in place.

Industry groups should be encouraged to contribute to and assist in the management process.

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Management of access

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Abstract

The management of access is critical in minimising the spread of *Phytophthora*. Recreational activities on CALM-managed lands present much greater risks than those posed by commercial operations which are licence or permit based. This is because the latter are more strictly supervised, and non-compliance with licence conditions can have implications for ongoing activities. In our management of access we attempt to balance the competing demands for requirements of access versus the need to protect areas from introduction of *Phytophthora*. With our present state of knowledge it is necessary to control access very strictly on some high value areas. This means total exclusion or permit based entry to *some* areas. It appears that in general the issue of management control of *Phytophthora* is still viewed by the public and local government as a State government problem which is mostly too hard for others to address. Main Roads (Western Australia) have procedures which review the cost/benefits of incorporating management in their programmes and make decisions on implementation based on risk and final cost. Main Roads will also assist Shires in developing dieback management techniques in road construction and maintenance. The management of access in relation to *Phytophthora* requires significant resources in planning such as the cost of management procedures and costs incurred by industry to meet standards imposed.

Management options that can be implemented to minimise introduction or spread of the fungus on 2WD and 4WD gravel roads are:
- improvement in the surface formation and drainage,
- demarcate existing disease areas associated with roads,
- manage maintenance according to hygiene standards,
- use seasonal or permanent closure as a means of protecting areas, and
- establish clean down stations at entrances to national parks and other areas of high conservation value.

For foot access on managed paths:
- limit activities with the potential to spread the fungus into dieback-free areas,
- use techniques such as surface hardening or boardwalks to reduce spread of infected soil,
- careful selection of alignment,
- implement seasonal closure,
- close permanently if high values are at risk,
- use strategically-located boot cleaning stations, and
- provide information.

Introduction

Other papers in this issue have provided a wide ranging overview of plant diseases in WA and the extent to which they are influencing our environment. The management of plant disease affecting native vegetation in WA has focused primarily on *Phytophthora* and in particular *P. cinnamomi*. This focus is due to the widespread distribution and the high level of impact the fungus is having on native vegetation throughout the South West. This paper is confined to the management of access in relation to plant disease, caused by *Phytophthora* spp.

Access is recognised as being one of, if not the, crucial factor in the artificial spread of the fungus in the south-west of Western Australia and it continues to be a critical and often contentious issue when considering the management objectives for land set aside for conservation. The issue is contentious because the management of access is really about the management of people and trying to accommodate their needs/wants against land management objectives for an area. The definition of access according to the Oxford Dictionary is: "**approach**; *(to) right or means of approaching or reaching*". To many (West) Australians, access particularly on Crown lands has been considered an inalienable right. Where access didn't exist it was created. The age of the 4WD vehicle has provided equivalent motorised opportunity to match that previously enjoyed by horsemen. In many respects we are talking about a cultural ethos with which many landowners, local authorities and management agencies have had to come to terms in the last 20 years or so.

Management of access can be looked at in terms of
1. lands managed by CALM (including State forest), and
2. lands other than those set aside strictly for the purpose of

conservation, *i.e.* the management of roadsides as well as other reserves and vacant Crown land set aside for a different purpose and managed by authorities/bodies other than CALM.

Conservation lands

Phytophthora/dieback is currently considered to represent the greatest single threat to the conservation values in the south west of the State in the short term. In the longer term, other factors such as the influence of climatic change may be important (but difficult) to manage! As a result of this, CALM and non-government conservation groups are concerned that management should be directed toward preventing the introduction of the fungus into areas not currently infested, or minimising its spread where it is already present or carrying out some control measures to protect species or communities from the fungus.

This sentiment is strongly presented in the CALM Policy (Conservation and Land Management 1991a) which states as it's objectives:
- to minimise the introduction, spread or intensification of the plant diseases caused by *Phytophthora* species throughout the State, with particular emphasis on the south-west,
- to monitor for *Phytophthora* activity in the remainder of the State, including tropical areas,
- to undertake and support research into the disease and its control, and
- to encourage the West Australian community to share our concern over the problem, and its management.

These key objectives, however, must also recognise that one of CALM's three primary programmes is recreation (Conservation and Land Management 1993a). Provision of access is obviously a significant component of this programme which can often be in conflict with other objectives. In addition to this there are also requirements to accommodate access for a range of government approved activities, such as
- timber production in State forests,
- mining exploration and mining,
- commercial operations *e.g.* apiarists, wildflower picking,
- research activities,
- fire protection needs, *i.e.* firebreaks, *etc*, and
- construction and maintenance of roads and powerlines.

The development of access carries with it other implications for the management of disease. These include the source of road making materials, the dieback status of these materials, and drainage control.

To deal objectively with the issues that arise in making decisions about differing needs for access, there is a requirement for effective and practical guidelines. These are generally provided by the Department of Conservation and Land Management's dieback policy, Regional Management Plans, Area Management Plans and Dieback Protection Plans, and are dealt with more specifically by separate procedures for mining and commercial activities such as timber production, bee keeping, wildflower picking and research activities. To be able to make decisions about access there is a need to have good information about where the disease is, the risk of introducing the fungus during an operation; chances of it surviving if it is brought in; the impact it may have. Some of

these questions resolve themselves into the concept of 'hazard' which is defined as the final impact of *Phytophthora* on a site if introduced. Obviously in areas where the hazard and the risk of introduction are low the options to manage are somewhat broader compared to where the hazard is, say high to very high.

For the following discussion we propose to direct our comments to the area within the defined *Phytophthora* zone in the south-west, where we are dealing with a high to very high hazard.

Recreation access

The most complex and trying aspect of access management is that related to recreation pressures. This is because management strategies need the co-operation of a large number of mostly unsupervised visitors to be effective.

Recreational access can generally be considered in terms of 2WD access, 4WD access, foot access, and other access, *i.e.* horses, cycling.

2WD roads

Sealed roads, once in place, do not present a high (but there is some) risk to vehicle traffic spreading the fungus. If the area which is traversed by the road is dieback-free then management of roadside operations should be conducted with careful attention to maintenance practices. If the alignment was infected prior to sealing then, intensification is likely due to roadside runoff and drainage.

Unsealed roads can present a considerable concern for management since roads external to a reserve may be managed entirely differently to roads within a reserve. Therefore, with no guarantee of hygiene on roads outside of a conservation reserve, there is a considerable risk that the fungus will be either introduced or spread by vehicles moving into the reserve.

In parks, Gazetted roads not under the control of CALM present similar concerns. In the case where a gravel spur road leaves a sealed road, the options presented also apply. If the alignment is not infected initially then risk of infection would be low, particularly if construction was undertaken under strictly controlled conditions.

The management options on **existing** roads are:
1. have 2WD roads in good condition and well drained,
2. identify disease areas and manage the road to limit the risk of picking up infected soil, *i.e.* with use of culverts; raising of road, crowning of road,
3. conduct maintenance operations in dry soil with attention to demarcating disease areas within catchment boundaries according to hygiene standards. (Conservation and Land Management 1986),
4. impose seasonal access restrictions (such management options can be difficult to implement because of inconsistency in weather conditions from year to year.),
5. impose closures based on conditions which present a high risk This can be difficult to implement in remote locations because of distance and unpredictable response of people who have travelled a considerable distance to get there, such closures must also consider people who

may already be at a site served by a road that is proposed to be closed, and

6. establish clean down stations at boundaries where roads are subject to different management regimes. Such options have been considered at places like the Fitzgerald River National Park, however the costs and practicalities of such facilities have discounted their use to date.

In situations where:

• there is no complementary management on existing roads that are serving a reserve, and
• where dieback hazard is high to very high, and
• dieback is in the general area,

then there is a high degree of inevitability that the fungus will be transported into an area. This is because management capability in keeping *Phytophthora* out of an area depends on the success of all phases of operations over a long time including the impact of changing personnel on continuity of work standards. This is therefore a system in which the risk of a breakdown of procedures is high.

4WD access

If the fungus is known from nearby and conditions are suitable, then 4WD access is a particular concern because the nature of these roads usually means that drainage is a problem and therefore the risk of moving infected soil can be high at particular times throughout the year.

The options for management are:

1. permanent closure and rehabilitation - if this is the best way of meeting management objectives, *i.e.* values are very high.
2. continue use - if the alignment is already exhibiting the impact of the disease it may be possible to continue use if this does not place substantially more vegetation at risk. Additionally, if there is concern/risk in taking infected soil away from the road then control over the timing of access may be appropriate.
3. seasonal closure is an alternative which can deal with the situation where access conditions and risk change dramatically with change of season.
4. "opportunistic" closure which is event linked. This option is good only if the area can be easily serviced by management, *i.e.* accessible immediately after the event which is likely to cause concern for access, and therefore enforceable.
5. Upgrading of 4WD standard roads often leads to 2WD standard.

Foot access

Unmanaged foot access can lead quite rapidly to erosion on slopes greater than 3%, (Lands, Park and Management 1987). In addition management of foot access can be an important issue where introduction or spread of *Phytophthora* is a concern. There is a considerable amount of circumstantial and substantiated (from sampling) evidence to demonstrate the spread of *Phytophthora* by foot traffic, particularly along the south coast. Once introduced to areas high in the profile, the potential for extensive damage is quite significant, as is ably demonstrated by the situation in the Stirling Range National Park.

Management of foot access has been based on:

1. mapping of disease occurrence,
2. identification of areas apparently not affected,
3. limiting current activities which have the potential to spread the fungus into areas identified as apparently dieback free,
4. using simple techniques to reduce the risk of taking infected soil upslope (or further along a path) *i.e.*
   — improve the path surface, *e.g.* use of stone to harden surface; boardwalks to avoid high risk areas
   — use clean down stations,
5. identifying the best location for the alignment, *i.e.* one side of a ridge,
6. monitoring dieback status,
7. implementing seasonal closure if the risk warrants it, and
8. permanent closure of paths if high values are at risk.

The key to reducing the risk in high hazard environments where it is necessary (or preferable) to provide a path is to

• provide a good alignment,
• provide a good walking surface,
• ensure adequate drainage, and
• engineer to minimise boggy/wet patches.

Information and public feedback

Management action must be supported by information to the users of lands to gain their support, understanding and co-operation in relation to managing access. Signs alone don't do the job and there aren't enough people on the ground to educate and enforce different measures.

Actions undertaken to control access in conservation lands for the management of *Phytophthora* are not always popular when first introduced. This is because they inevitably conflict with existing/traditional activities. Despite the volume of written material published and that presented through the television and radio media, the depth of understanding of the public concerning the issue is very shallow. This is quite understandable when considering the difficulty in coming to grips with an invisible fungus that in most cases can only be recognised from where it's been (*i.e.* dead plants), the fact that impacts can vary from dramatic in the short term to incremental over a long time (and most don't see them anyway), and that for most people the issue doesn't directly affect them to any great degree. It really falls into the category of an "SEP" (Someone Else's Problem). This difficulty in coming to terms with what the presence of the disease may mean to plant communities and environment as a whole in even the short to medium term (*i.e.* 1-5 years) is clearly evident in reviewing the public response to draft management plans for conservation areas.

Generally, public perception and response with regard to *Phytophthora*, its impacts and the measures taken to control its spread in areas managed for conservation seems to be:
• the issue exists (some disagree) and
• sure, we should do something about it, and
• management actions are basically OK as long as they don't affect what I want to do!

Access is always a contentious issue in the planning process, especially where a history of existing use is in evidence. An extreme view on the South Coast is that CALM

invented dieback so it could interfere with people's enjoyment of National Parks. There is also a view expressed by a minority that key conservation areas should be closed to any access.

We do not have the answer to the question of "how do we overcome this?" At the moment, the depth of understanding and concern that individuals have over this issue is closely related to the extent that they are involved in it. If people don't want to know, or aren't interested, then it is unlikely any approach other than enforcement will be effective. Education of the younger generation in schools is possibly the best option, but by the time they are old enough to influence the situation the issue is probably going to be all over.

It really is a matter of the extent we want to protect and more importantly retain, the diversity and values of our native vegetation.

Other activities in conservation lands

As stated, the Dieback Policy really sets out how we should go about managing access. In addition, there are specific guidelines for other more commercially oriented activities.

— Timber Production. The set of prescriptions in "Timber Harvesting in WA" (Conservation and Land Management 1993a) very clearly sets out the standards for roading and conditions under which access is provided in State Forests.

— Parts of State Forest are still included in Disease Risk Areas where access controls are prescribed. These areas were originally gazetted for a period of three years to allow for mapping of dieback disease, during which time access controls were stringently enforced. This system is now being reviewed.

— Apiary activities are addressed by a CALM policy statement (Conservation and Land Management 1992). This includes guidelines on how vehicle access is to be managed and who bears responsibility for costs incurred to ensure ongoing access availability.

— Wildflower picking is conducted under a Commercial Purposes licence under the Wildlife Conservation Act which includes specific instructions on access, in particular on land tenures such as State forest. Wildflower picking is not allowed in Nature Reserves and National Parks. Management of illegal picking has been a major problem in the past and still continues to be an issue of concern.

There are considerable risks associated with managing a wildflower industry based primarily on Crown lands despite a licensing condition specifying the use of existing tracks only. The indiscriminate creation of new tracks and access has lead to the recent removal of *B. baxterii* and *B. coccinea* from the picking list, because of the threat that *Phytophthora* now presents to these species in all Crown lands.

Research

Access for research purposes must also conform to the standards that are applied to other land users. This can mean that research proposals have to be amended. These aspects are dealt with in assessing research proposals both for inter-

nal and external research programmes. In the past there is no doubt that intensive research programmes have contributed to disease spread. No group of users is immune from having the capability of being a vector of the fungus.

Management activities

Management operations and personnel similarly have the potential to spread the fungus and therefore regular training and adherence to procedures is essential. The Hygiene Evaluation Test is a critical tool to ensure the right questions are asked about any proposed operation (Conservation and Land Management 1993b).

Mining

The State government's mining policy sets out the procedures under which all proposals are assessed. These procedures include referrals to CALM and the Minister for the Environment to consider whether standard conditions are adequate to address environmental concerns. Access (timing, method, degree of disturbance) is a critical issue in the assessment of proposals. New access (grid lines, *etc*) created by legal operations can provide opportunities for unauthorised access by people who are unaware of the strict conditions under which such access was developed and utilised. The conditions which are applied to mining and petroleum operations, particularly exploration activities are quite strict and with respect to dieback controls, are from my experience usually well managed.

Summary

In respect to Conservation land then, there is a significant difference in the management of access for recreation as opposed to the more commercially-based operations. This is because the commercial operations usually involve small number of people who have been longer in the job, are better trained, are involved with localised areas, and are either licence or permit based which carries implications for non-compliance with conditions. They are usually supervised to some extent by CALM staff.

The key point about management of access is that all the various options
- cost money to carry our according to the standards set,
- need compliance to work,
- need management presence/supervision, and
- need to be regularly monitored.

Much of the access network in conservation lands is managed in the absence of these points. We are not able to provide the money required or the supervision needed to ensure compliance.

Management of access on other lands

No other agencies currently manage lands with the objective of controlling or minimising the introduction or spread of *Phytophthora* through control of access. Those who do carry out some management include some of the mineral sands mining operations over their lease areas.

To date, few local authorities have been able to develop policies and address dieback issues in their planning of proposed road works despite the fact that a format for such a document has been prepared by CALM and provided to local authorities on request. Despite being approached through the country Shire Councils Association to develop an approach to dieback, it would appear that the issue for local government authorities is just,

- too hard, and/or
- too expensive, and/or
- is perceived to be unnecessary by some.

There are a number of difficulties confronting local authorities in dealing with this issue. They are:

- recognition of the disease,
- survey and sampling costs,
- skills,
- operational costs,
- administrative hassles.

The most active and structured program is that being developed by Main Roads WA (Napier 1992). With over 3000 km of roads within the dieback susceptible areas of the State, Main Roads has a large task with specific problems facing them in the management of roadside areas. However the department has the will and technical expertise to work towards dealing with the issue. Five categories which influence the management of roadsides have been identified by MRWA:

1. uncontrolled access,
2. road drainage,
3. on going maintenance,
4. gravel supplies, and
5. dieback mapping.

These various factors must be taken into consideration when assessing and planning an operation to see if the balance of "benefits" from undertaking controls of Dieback are worth the costs and effort.

Decision-making flow-charts have been developed to assist in the assessment of proposed works and the selection of relevant Dieback controls. Knowing the extent of the disease over the road network is a primary requirement for their program to proceed and contributes to the management of *Phytophthora* on more than just a local level. However, application of dieback management to all possible activities which may spread the fungus is proving extremely difficult, *e.g.* hygiene procedures for maintenance grading over long sections of road shoulder. This is proving expensive and often impractical and it is difficult to identify any positive value from the work because of the unknown dieback status and history of most of the roadsides. As with all groups concerned with doing something to ameliorate the threat of *Phytophthora*, there is always a concern that unless more stakeholders are involved and show a similar readiness to make real efforts then the efforts of an individual group will be greatly jeopardised or worse, be a waste of effort.

Case studies

Stirling Range National Park

A considerable proportion of the Stirling Range National Park has been affected by *Phytophthora cinnamomi*. It is apparent that the combination of soils, rainfall and a diverse

susceptible flora has provided a situation very conducive to the survival and activity of the fungus. Most vegetation types are severely affected. The wandoo woodlands, however do not exhibit symptoms of the disease due to the lack of susceptible species.

Over the last eighteen months considerable effort has been directed at identifying those areas apparently dieback free, particularly in the higher peaks. Current information suggests that few areas of protectable dieback free vegetation exist on the higher peaks. There do however appear to be considerable areas, including some of the lower peaks that are apparently die-back free. It seems likely that those areas have remained free of *Phytophthora* because they have offered less of an attraction for bushwalkers and other activities that have been conducted in the park.

Various options have been considered to protect vulnerable areas from introduction of the fungus. The use of boardwalks and clean down stations such as at Mondurup Peak are one means of trying to minimise the risk of introduction of the fungus. The situation as presented for Stirling Range National Park is now being considered during the Management Planning process. The question of how to deal with access throughout the park is, as usual, complicated by the competing demands of park users.

Fitzgerald River National Park

The distribution of *Phytophthora* spp in the Fitzgerald River National Park was presented in the Fitzgerald River National Park Management Plan (Conservation and Land Management 1991b). This map was based on up to date information at the time and showed the distribution of both *P. cinnamomi* and *P. megasperma*. The difficulty of recovering *P. megasperma* from apparent disease sites and the impact of the 1989/90 fires which affected many previously suspect sites resulted in many areas being identified as "suspect" in the plan, relying on future monitoring to clarify the situation. Very wet years in 1992 and 1993 initiated widespread symptoms of *Phytophthora* activity in both eastern and western ends of the park and this has been subsequently confirmed by sampling recoveries of *P. megasperma*. It is now apparent that *P. megasperma* is present extensively along some road sections in the Fitzgerald River National Park and that these infections are probably quite old.

Management operations in the park, particularly since 1986, have been conducted under strict hygiene based on the premise that most areas were dieback free. The recent revelations have highlighted the difficulty of managing road systems that were in place prior to vesting. In this situation we have identified spread of *Phytophthora* from infections on old alignments that have been closed to traffic for over a decade. The implications for management is that any work on these road sections which may result in conditions suitable for the fungus (such as drains/culverts) will probably result in 'new' areas of disease expression. The intermittent behaviour of the fungus also makes monitoring of operations much more complicated.

The picture in the Fitzgerald River National Park is far from clear and highlights the need for better understanding of *P. megasperma* in this environment and its potential long term impacts.

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Control options of plant pathogens in native plant communities in south-western Australia

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Abstract

Control of plant diseases in natural communities can involve management practices such as hazard rating, hygiene measures, quarantine, chemical applications, plant breeding, biological control agents, and molecular manipulations involving hosts, pathogens and beneficial microorganisms. This paper will examine traditional, immunological and nucleic acid-based methods for the detection, identification and control of plant pathogens and their application in native plant communities.

Introduction

The plant diversity of south-western Australia is unique, with some 9,000 plant species, many of which are endemic. As many as 2000 species may be susceptible to *Phytophthora* species (Wills 1993), and many more are susceptible to other pathogens. Natural ecosystems are important centres of biodiversity and are important assets for tourism, recreation and conservation. The management of plant communities to maintain their intrinsic value includes disease control.

Considerable worldwide research has concentrated on the control of plant diseases; however, the majority of this work concerns economically important crop plants. Crops are usually grown in monoculture on a broad scale under well-fertilised, weed-free, and often, irrigated conditions. The plants are usually selected lines, bred for uniformity in germination, growth, crop maturity, and yield; in addition, cultural conditions are usually reasonably homogeneous. This compares with the huge diversity of plant species, uneven distribution of individuals, genetic variability, soil types and micro- and macro-environmental conditions present in a natural ecosystem.

There are many ecological differences between agricultural and natural ecosystems, and those that set them apart embrace the concepts of population size, density, and spatial distribution, genetic variability in host populations, and population continuity or predictability through time (Burdon 1993). In natural ecosystems, plants are adapted to their pathogens; those that are not adapted are replaced by those better adapted. If a plant becomes unusually plentiful, because of favourable conditions, its parasites increase with it and reduce the fitness and subsequently the number of susceptible plants, which in turn results in a reduction in the numbers of the parasite. The population of an organism in a given ecosystem is under continuous adaptive selection, through interaction with other organisms, for greater fitness

(Cook & Baker 1983). It immediately becomes apparent that enormous complexities are involved in applying any control method in a natural, compared to a cultivated, system.

Epidemics of plant disease in natural plant communities are relatively commonplace; examples include outbreaks of *Albugo candida* and *Peronospora parasitica* and their effects on the survival of *Capsella bursa-pastoris* (Alexander & Burdon 1984), and flax rust *Melampsora lini* on wild flax *Linum marginale* (Burdon & Jarosz 1992). The occurrence of a plant disease epidemic in a natural community indicates that some aspect of the ecosystem is not in balance. A number of essential changes need to occur for disease outbreaks to occur (Cook & Baker 1983):

1) the pathogen is genetically homogeneous, (implies introduction) and highly virulent, in high inoculum density or is not in balance with its antagonists;

2) the abiotic environment is relatively more favourable to the pathogen than to the host and/or the antagonists;

3) the host plant is genetically homogeneous, highly susceptible, and continuously or extensively grown (as in cultivated crops); and

4) the antagonists are absent or in low numbers, lack suitable substrate or the proper environment to function as antagonists, or are inhibited by other microorganisms.

Therefore, in cultivated crops plant diseases can be endemic or introduced. In a natural community pathogens are usually introduced or alternatively environmental factors have changed (due to man or nature), that predispose plants to a pathogen. Therefore, it is important to consider in detail the classical disease triangle (host-pathogen-environment), when considering a plant epidemic in a natural ecosystem.

In Western Australia, most of the "natural" ecosystems have been changed in some way, through such influences as forestry, wildflower picking, fire management, mining activities, road building, bushwalkers, clearing farmland and hydrological changes due to many of these activities. These can all affect the biological equilibrium and result in disease outbreaks. It is often hard if not impossible to associate such changes with a disease outbreak, if the pathogen is proven not to be introduced. Therefore, our information base on our

knowledge of any potential endemic or introduced pathogens needs to be extended. This includes their specific requirements for survival, means of dissemination, host range, infection processes and pathogenicity. These requirements are further influenced by climatic changes (on pathogen and host), by human activities (management, economic and casual), or by fauna activity (defoliators and borers).

It can still be argued that many areas of the biology, ecology and pathology of most if not all pathogens (including *P. cinnamomi*) are not well understood and, until this is so, the appropriateness of many control strategies such as biological and chemical control or burning are questionable. Therefore, the main priority in controlling a pathogen is to have a comprehensive understanding of its biology, ecology, pathology and host range. For example, although many assumptions are made about the importance of chlamydospores and oospores as survival structures, it is still to be conclusively shown for most *Phytophthora* species that these survival structures are produced naturally in soils and plants and, if so, how long they survive and how readily they germinate. Considerable research has been done *in vitro* and *in vivo* on propagules that have been artificially produced on or in rich artificial media and then placed into soils under various temperature and moisture regimes. How these survival structures relate to those that are produced naturally is not known. For example, oospores of *P. citricola* which were produced axenically in V8 broth cultures had very short survival times compared to those produced in non-sterile soil extracts. Those produced in non-sterile soil extracts survived many months (Hardy, *unpublished data*).

In this paper control options have been divided into five main groups cultural, resistance, chemical, biological and molecular strategies.

Cultural control options

Cultural control options aim to restrict the spread and reduce the amount of inoculum. In natural ecosystems such as the forests, heathlands and the banksia woodlands of the south-west, one potential control strategy is manipulation of the environment with fire management. Once the biology and ecology of existing pathogens and the ecology of hosts are known, fire could be used to successfully reduce inoculum levels. However, one consequence of using fire may be to provide infection via wounding by other pathogens, particularly aerial ones. Quarantine measures are also effective in reducing the spread of soil-borne plant pathogens, particularly for introduced pathogens, such as *P. cinnamomi*. For aerial pathogens, quarantine is of little value since they can be spread great distances by wind which cannot be controlled by quarantine. Cultural techniques should be explored for the control of plant pathogens in natural ecosystems, especially for those plants which are endangered.

Resistance

Induced resistance or immunisation

Recently, immunisation (cross protection) against plant disease has been well documented for a range of pathogens in widely diverse plants and plant tissues (Kuc 1990). Plant immunisation has proved successful in expressing, or sensitising for expression, resistance mechanisms in plants which are considered economically important. Induced resistance essentially involves infecting plants with an avirulent isolate of the pathogen, or a non-related pathogen which induces a host resistance response. This in turn effectively stops the invasion of the pathogen in question. The induction of resistance in tobacco to tobacco mosaic virus with specific chemicals such as salicylic acid and methyl-2,6-dichloroisonicotinic acid has been shown (De Waard *et al.* 1993). Such techniques may in the future be useful for the control of certain plant diseases in natural systems, such as the preservation of rare and endangered species.

Plant breeding for resistance

Breeding for resistance in natural ecosystems where there is a large diversity in plant species is not practical, due to associated costs of developing and introducing resistant plants. The only areas where it would be practical would be to preserve specific attributes of rare and endangered flora and in rehabilitation of severely denuded areas (mass collapse sites and rehabilitated mines). This topic is covered by McComb *et al.* (1994).

Chemical control

Chemicals were used to control plant diseases long before their causal agencies were known. They have been effectively used in intensive agronomic situations, but the control of plant pathogens in native plant communities by chemicals is generally not practical due to costs of the chemical(s) and their application. Possibilities of phytotoxicity, resistance, effects on fauna and other beneficial fungi need to be considered. It is possible that the use of fungicides can tip the balance in favour of opportunistic pathogens. In such instances, the use of fungicides at very low rates in conjunction with other factors may be beneficial.

In natural communities, systemic fungicides (which enter the plant, become generally distributed within it, and render the tissues resistant) to attack are the only real chemical option. Most systemic fungicides currently on the market are translocated in the apoplast (Manners 1993); therefore application of systemics is likely to result in their being extensively distributed, via the xylem, throughout the plant. Conversely, application of fungicides to the soil as drenches or seed dressings will not be practical in an extensive and diverse natural environment. However, this should not preclude their application in certain instances or stop further research on their use.

Recently research has shown that the use of neutralised phosphorous acid, which is inexpensive, has low toxicity to plants and animals and has high mobility within plants, will have considerable value in the conservation of rare and endangered plant species (Shearer *et al.* 1991). However, on a broad scale, costs of application, differing tolerances of plant species to this chemical, and side effects on invertebrates and other fungi, need further research. It is possible that frequent use might lead to the selection of resistant pathogenic strains to the chemical (Cohen & Coffey 1986, Coffey 1991), although there is no evidence of resistant strains developing during the last decade of use (Guest & Grant 1991). In addition, *Phytophthora* species differ in their

tolerance or susceptibility to the chemical, which could give a locally competitive advantage to other *Phytophthora* species in the area. For example, *P. megasperma* is relatively insensitive to the chemical (Dercks & Buchenauer 1987), and is present in areas where *P. cinnamomi* also occurs (Bellgard, *pers. comm.*), such as the Fitzgerald River National Park. Therefore, caution needs to be exercised before phosphorous acid is used extensively in an area. In addition, phosphorous acid does not eradicate the pathogen; it activates the plant defence systems which then stop the spread of the pathogen within tissues. Perhaps the best use of phosphorous acid would be its application for the preservation of rare and endangered plant communities. Additional research is required to clearly determine the exact mechanisms involved in disease resistance after the application of phosphorous acid.

Many fungicides have different effects on a fungus depending on the structures it comes into contact with. For example, a number of fungicides sold for the control of *Phytophthora* species have no effect on endogenously dormant oospores of *P. citricola* and *P. megasperma*, whilst hyphae are killed (Hardy *et al. unpublished data*). These oospores could not be induced to germinate in the presence of the fungicides, but would do so once residues of the fungicides had disappeared. It is possible that such effects might occur with other resting structures such as chlamydospores. Therefore, it is necessary to have an understanding of the effects of a particular fungicide on all stages of a fungal life cycle before it can be used with complete confidence.

Improved knowledge of fungal biochemistry should allow a more rational choice of fungicides, and open the way for the appropriate resistant genes to be cloned and their role in metabolism and pathogenicity explored (De Waard *et al.* 1993).

Biological control

Biological control has been defined as "the reduction of the amount of inoculum or disease producing activity of a pathogen accomplished by or through one or more organisms other than man" (Cook & Baker 1983). The mechanisms of biological control can be grouped into two categories: 1) the use of antagonistic microorganisms, either resident or introduced to reduce the pathogens population level; this includes avirulent or hypovirulent individuals or populations within the pathogenic species itself; and 2) protection of plant surfaces against infection, by genetic manipulation of the plant and the use of specific cultural practices (Cook & Baker 1983).

There are three mechanisms by which biological control may operate in the infection court (rhizosphere or phylloplane):

1) parasitism and predation: there is active contact between microorganisms which result in the degradation of hyphal walls or mycophagy of whole propagules;

2) amensalism: the biological control agent produces antibiotics or toxic metabolic by-products which inhibit the growth of the pathogen; and

3) competition: involves two or more microorganisms competing for the same limited resource, such as oxygen, space, nutrients and moisture.

It is very likely that successful antagonists employ more than one of the above strategies.

The major stumbling block for applying a biological control agent in the field is that the environmental niche into which it is being applied is most likely already occupied. Therefore, a niche for the biological agent needs to be established (Powell *et al.* 1990). Formation of a niche for the bioagent can be accomplished in a number of ways: the biological agent

1) could utilise a substrate not currently used by other microorganisms;

2) may be better adapted physiologically for a particular niche than are the microorganisms currently occupying it;

3) produces an antibiotic which through its activity creates a zone of substrate possession around it;

4) the biological agent is applied with or after a physical or chemical treatment that decreases the indigenous microflora; and

5) is added to the environment in such a form that large amounts of new substrate give it a head start over the indigenous microflora.

A successful biological control agent is likely to employ more than one of the above conditions. However, in natural ecosystems, as with the application of chemicals, costs of application will be high. There will be associated problems with how the control agents are applied, and in the case of soil-borne plant pathogens, how they can be incorporated into the soil profile where they will be effective. In addition, selection of biological agent(s) that can survive and function across a broad environmental range (differences in moisture, temperature, pH, fertility, host range, soil types and micro-environments) and plant communities would be difficult. It will be necessary to obtain a good understanding of the host-pathogen-biological control agent-environmental interactions before the biological control agents can successfully be applied in the field. There is a general misconception that a biological control agent should eradicate a pathogen, but even a balanced equilibrium between a pathogen and its antagonist(s) should be considered beneficial.

dsRNA for the control of *Phytophthora* species.

Many fungal species have been found to contain double stranded RNA viral genomes in their cytoplasm. These have assumed a great deal of importance in recent years with the discovery that these elements attenuate the virulence of the fungal species which cause chestnut blight (*Cryphonectria parasitica*) and dutch elm disease (*Ophiostoma ulmi*). In both of these diseases, dsRNA-containing hypovirulent strains are able to protect the host trees against attack by virulent strains. Protection occurs via transmission of the dsRNA element to the attacking virulent strain converting it to a hypovirulent strain.

The dsRNA elements of *C. parasitica* are the best characterised and studied. Hypovirulent isolates of *C. parasitica* contain a number of dsRNA segments (Nuss & Koltin 1990, McDonald & Fulbright 1991). The number of segments, size and sequence homology may vary between strains. Comparison of dsRNA from an American and a European isolate of *C. parasitica* revealed that each contained a large dsRNA of

about 12 kilobases in size, and a number of smaller dsRNAs that were derived from the large dsRNA. The number, size, and concentration of the smaller molecules varied with the strain and stage of growth (Nuss & Koltin 1990). Polypeptide coding sequences occupy only a small part of the element. *Ophiostoma ulmi* isolates contain a specific set of 10 dsRNA segments ranging in size from 0.34 to 3.5 kb which are associated with transmissible hypovirulence. Not all segments may be transmitted, and healthy isolates recovered from a diseased isolate were found not to contain segments 4, 7, and 10 (Nuss & Koltin 1990).

The discovery of these elements in *C. parasitica* and *O. ulmi*, and their association with the hypovirulent state, spurred a search for similar hypovirulent elements in other species of phytopathogenic fungi with the hope that they could be used as biological agents to control disease. dsRNA elements have now been found in both highly and weakly virulent isolates of the wheat pathogen *Gaeumannomyces graminis* var *tritici* (Nuss & Koltin 1990). However in studies with hypovirulent isolates it was found that virulent isolates could segregate out and that these were free of dsRNA elements, whereas the hypovirulent isolates retained the dsRNA. Isolates of the fungus *Helminthosporium victoriae*, which causes oat blight, have been found to contain dsRNA viruses; one is associated with hypovirulence (Nuss & Koltin 1990). Hammar *et al.* (1989) detected a multisegmented dsRNA element in a hypovirulent isolate of *Leucostoma persooni*, and showed that the elimination of these elements restored virulence. In an elegant series of experiments, Sonnenberg & Van Griensven (1991) showed that La France disease in *Agaricus bisporus* is due to the transmission of a multisegmented dsRNA from a diseased to a healthy isolate by hyphal anastomosis. DNA markers were used to show that there was no transmission of either nuclei or mitochondria between the strains.

In spite of the evidence that dsRNA confers hypovirulence to fungal isolates there are instances where they may enhance virulence, or have no effect. Tooley *et al.* (1989) studied the distribution of dsRNA elements in isolates of *Phytophthora infestans* and found that 36% of Mexican isolates contained dsRNA. However there was no correlation between the presence of dsRNA and virulence. Studies with *Rhizoctonia solani* have reached different conclusions. Castanho & Butler (1978) isolated three segments of dsRNA from a diseased isolate of *R. solani*. Healthy isolates recovered from this diseased isolate by hyphal tip culture did not contain dsRNA. In plate tests it was shown that the diseased isolate could protect plants against the healthy isolate. However, Finkler *et al.* (1985) compared virulent and hypovirulent isolates of *R. solani* from Israel, and found that only the virulent isolates contained dsRNA. Transmission of virulence to a hypovirulent strain was found to be associated with transmission of the dsRNA. More recently Bharathan & Tvantzis (1990) found dsRNA in all isolates tested from diverse locations in the USA and Canada. Isolates from 5 anastomosis groups (AG) representing a wide range of virulence were included in the study. There was a high degree of heterogeneity among dsRNA's from the same isolate, or from isolates within the same AG. This was especially evident in AG4, dsRNA's from these isolates were highly specific for the isolate from which they came indicating a lack of horizontal transmission of genetic elements in this AG. Cross hybridi-

sation did occur among dsRNA segments from 3 hypovirulent isolates belonging to AG's 2, 3, and 5, suggesting that there may be a sequence involved in suppression of virulence. However, the results show that overall there is no correlation between the presence of dsRNA and virulence. Similar conclusions were reached in a study of wheat infecting isolates of *R. solani* AG8 in Western Australia (Yang *et al.* 1994).

What are the prospects for the use of dsRNA elements in biocontrol of pathogens such as *Phytophthora*? Theoretically the use of dsRNA elements for biocontrol of *Phytophthora* is possible. The biocontrol agent would colonise the same microhabitat and is subject to the same influences as the pathogen. Moreover, since the antagonist converts the pathogen to an antagonist, the level of control will not decrease (provided that the dsRNA is not debilitating). Studies on the distribution of dsRNA elements suggest that they are widespread, and that there should be no trouble finding them in isolates of *P. cinnamomi*. However, not all of these would be expected to be hypovirulent, and in fact some may be hypervirulent. Hypovirulent elements also have the additional disadvantage that they may debilitate the host strain making it less able to withstand competition from other microflora. This would result in the eventual disappearance of the strain from the environment. The results of previous studies suggest that we would be lucky to find a hypovirulent element which could be effectively used as a biocontrol agent. How do we decide which dsRNA elements we should use? The elements should not severely debilitate the host strain, and should be capable of being transmitted to other strains from the same species despite incompatibility barriers between the strains. The elements should be stably maintained in different genetic backgrounds. Finally, in deciding which elements are hypovirulent it is important to take into account the level of genetic variation between host strains. Hypovirulent factors are identified by comparison of the pathogenicity of dsRNA containing and dsRNA free isolates. However, in this regard it is essential that the isolates being compared are characterised by means of DNA fingerprinting to ensure they are isogenic except for the dsRNA element. The application of DNA fingerprinting techniques has shown that isolates which look and behave the same are often quite different. Finally, if hypovirulence is shown to be an important form of disease control, there are the questions of how will it be introduced into the environment and how long it would take to function? These questions are particularly pertinent considering the huge and diverse areas of vegetation affected.

In the event that we do not identify a suitable dsRNA element for biocontrol, we still have the possibility of using dsRNA elements as delivery vehicles for dominant avirulent genes. These genes could be artificially-constructed antisense versions of pathogenesis genes, or naturally-occurring fungal avirulent genes. Using cloned fungal pathogenesis genes we can construct antisense versions of these genes in the laboratory, and insert these by gene splicing into dsRNA elements (to create a dsRNA*). Transformation of the dsRNA* into a strain of the target organism would create a biocontrol agent. Expression of the antisense version of the pathogenesis gene would inhibit expression of the sense gene thereby attenuating virulence. The dsRNA* would be transmitted to pathogenic strains in the same way as a naturally occurring hypovirulent element, and would convert those virulent strains to hypovirulent strains.

Molecular strategies for disease management

Molecular strategies available for disease control are primarily concerned with crops of agronomic importance. However, the use of molecular strategies of disease control in native plant communities will in the medium to long term provide beneficial tools in the area of disease diagnosis. The use of molecular techniques for early diagnosis, genetic manipulation of the pathogen(s), biocontrol agents and the host(s) hold considerable promise. However, increased funding into these techniques at the expense of traditional plant pathological strategies and ecological studies must not occur. It is imperative that these disciplines occur in conjunction with each other.

Diagnostics

The early and accurate diagnosis of plant diseases using molecular strategies, such as immunological techniques, and nucleic-acid based methods could become an integral management strategy of native plant communities. Management of plant diseases is most effective if control measures can be introduced at an early stage of disease development. Reliance on symptoms is often inadequate in this regard, since symptoms often appear long after disease establishment. Although biological techniques of disease diagnosis are usually very accurate, they are slow and not amenable to large scale applications. Molecular techniques of diagnosis must be viewed as management tools, to be used in conjunction with other diagnostic procedures, knowledge of the host, and an understanding of the ecology of the disease and the biology of the pathogen. For example, a pathogen may be detected in a locality but not cause disease due to one or more of the host, pathogen or environmental factors are not optimal for the disease to occur.

Molecular biology now provides rapid, specific, and sensitive techniques for detection of some plant pathogens. They will in the future become important early diagnostic tools for the early identification of plant pathogens.

Immunoassays in plant pathogen detection

Methods such as serological assays for pathogens, particularly viruses have been available for many years. Immunological assays include enzyme linked immunoabsorbent assays (ELISA), immunofluorescent assays, monoclonal and polyclonal antibody assays. Immunoassays have the potential to detect and quantify pathogen propagules in soil and other substrates. The role of an immunoassay is to reveal the presence of specific complexes between the antibody and antigen, that are unique to the pathogen. Immunological techniques can aid successful plant protection since they permit the early detection and correct identification of important pathogens. As many fungicides are specific only to certain pathogens or groups of pathogens, immunodiagnosis can help in the selection of the most appropriate fungicide treatment (Fox 1993). Immunological techniques can be used to quickly and accurately recognise and identify those pathogens with variable or latent symptoms on the host plant.

Nucleic-acid hybridisation based detection of pathogens

At present the exploitation of nucleic acids, DNA and RNA, in practical methods for the detection and/or identification of plant pathogens is in its infancy, and it will be a number of years before such methods will be of practical benefit. This is in comparison to the use of molecular methods in clinical pathology, or the use of immunological methods in phytopathology (Fox 1993). However, the potential advantages of this technology are overwhelming and it is inevitable that their adoption will be widespread. Nucleic-acid hybridisation depends on the high degree of specificity inherent in the pairing of nucleotide base sequences. This specificity allows the technique to be used for diagnostic purposes. The detection of plant pathogens via their nucleic-acids has two major advantages over rival technologies (Fox 1993). Firstly, all viable propagules (virus particles, spores, mycelium, *etc.*) contain the entire nucleic-acid complement of the organism. The presence of the nucleic-acid sequences is not altered by development or by response to environment or by the host. Antigens, in contrast may only be present at certain points in an organisms life cycle. In addition, the ability of the polymerase chain reaction (PCR) to detect one molecule of a particular sequence, conveys the ability to detect just one viable cell of the pathogen. This ultimate level of sensitivity obviates the need to culture pathogens prior to identification. Secondly, the identity of an organism is the direct result of the expression of its nucleic acids into protein and RNAs. Thus detection of a nucleic-acid sequence is simultaneously a positive identification. The nucleic-acid sequences in pathogens vary in their homology to sequences in other organisms. Thus it is possible to use nucleic-acid based methods for different levels of discrimination. For example, probes could in theory be designed which detect all fungi, or all ascomycetes, or all powdery mildews, or barley mildew or a particular pathotype in which one might be interested (Fox 1993).

Despite these positive features, nucleic-acid based methods are viewed with suspicion by many plant pathologists. They believe the methods are expensive, complex, slow and involve hazardous chemicals. It is therefore a challenge to plant pathologists to develop cheap, reliable methods suited to routine laboratories and even the end user (forester, farmer *etc.*). The techniques available include dot-blot assays, non-radioactive labels, restriction fragment length polymorphisms (RFLP's), nucleic-acid probes, cloned probes and synthetic probes.

The polymerase chain reaction (PCR)

This is a comparatively new method which relies on two specific DNA primers, a thermostable DNA polymerase and temperature cycling to amplify discrete regions of DNA. It is extremely sensitive with the theoretical potential to detect a single target molecule in a complex mixture without using radioactive probes; and it is rapid and versatile (Henson & French 1993). Unlike serology, synthesis of hundreds of different PCR primers generates costs comparable to those of developing only a few monoclonal antibodies. PCR is capable of quantifying relative differences as well as absolute amounts of scarce target DNA or RNA sequences. The quantification of plant pathogens in diseased plants is possible, since changes of inoculum levels in soil or plants can be monitored by PCR. This can help predict the potential severity of the pathogen and assist in control decisions.

PCR has considerable potential in epidemiological studies. It has the ability to be applied to studying disease resistance and determining at what stage of pathogenesis a

pathogen is inhibited. PCR can be used to estimate the biomass of unculturable microorganisms or obligate biotrophs. Microbial detection methods can be improved by combining PCR with antibody binding, this also gives a better indication of microbial viability. PCR is already being used to advance studies of host-pathogen interactions, such as for *Erwinia* (Blakemore *et al.* 1992), *Pyrenophora* (Reeves & Ball 1991) and *Leptosphaeria maculans* (Goodwin & Annis 1991). PCR could be used to construct pathogen genomic or cDNA libraries, or could be used to construct libraries of host or pathogen genes that are differentially expressed during the infection process.

As PCR methods for detection of pathogens become available, it will be possible to focus research on studying pathogen populations, biology, ecology, variability and host-pathogen interactions (Henson *et al.* 1993). An effective diagnostic test must be simple, accurate, rapid and safe to perform, yet sensitive to avoid 'false positives'.

Development of resistant plants by genetic engineering

In recent years plants resistant to viral diseases have been developed by genetic engineering. This has been achieved by inserting viral genes into the plant genome so that their expression inhibits the normal viral life cycle. This same strategy can be applied to a wide variety of plant viruses. Fungi are much more complex, and use a wider variety of mechanisms to achieve their colonisation of the host plant. Nonetheless we are beginning to identify the mechanisms used by fungi to infect plants. Once we have identified these mechanisms we can engineer the plant to these and thus confer resistance to these plants.

One approach is to use fungal inhibitory proteins. This does not depend on knowing the mechanism of infection. Genes for the proteins are inserted into the plant genome where they are expressed. In two separate studies plants resistant to *Rhizoctonia solani* have been engineered by inserting the chitinase gene from bean (Broglie & Broglie 1993), and the barley ribosome inhibiting protein gene (Logemann *et al.* 1992) into the plant genome. Both of these mechanisms on their own conferred higher levels of resistance to *R. solani*. These studies demonstrate the utility of the general approach of using antifungal proteins to engineer resistant plants. Many plant species contain antifungal proteins, be they lectins which bind to the fungal cell wall and inhibit growth, or enzymes which degrade the fungal wall.

Another approach would be to inhibit the enzymes produced by the pathogen and which are necessary for infection (Kotoujansky 1987). Many soft rot pathogens such as *Erwinia* produce pectic enzymes which breakdown the pectic substances producing the typical soft rot symptoms. Most of these enzymes produce oligogalacturonide degradation products which induce a defence response in the plant and thereby limit infection. Highly virulent isolates produce additional compounds which degrade these elicitors and prevent induction of the plant defence responses. These enzymes can be targeted by the use of polygalacturonase inhibiting proteins (PGiP) which have been described in all dicot species (Hoffman & Turner 1984). Potentially, by transferring the gene for such an inhibitor to the plant genome, the inhibitor would prevent colonisation by highly virulent strains.

A variation on this theme would be to use antibodies, or more correctly plantibodies. A number of studies have now demonstrated that we can now synthesise antibodies in plants (Pluclzltun 1992). This can be achieved by transformation with antibody synthesising genes. Antibodies against fungal extracellular enzymes or against the fungal wall components could inhibit infection of the host. Similarly, antibodies against detoxifying enzymes could be used to achieve resistance. The fungus *Nectria haematococca* is a pathogen of peas. The fungus produces the enzyme pisatin demethylase which inactivates the phytoalexin pisatin produced by the host (Schafer *et al.* 1989). The production of plantibodies against this enzyme would enable the host to limit colonisation by the fungus.

Genetic engineering of resistant plants can be achieved by using genes derived from the pathogen. Incompatible reactions between the pathogen and the host are determined by avirulent (avr) genes in the pathogen which act with genes in the host to induce defence responses and limit the spread of the pathogen. One novel idea suggested is to take the avr gene and place it in the plant genome by transformation technology (DeWitt 1992). The gene is modified in such a way that any infection would trigger it's expression. This in turn would induce expression of the host defence responses. Thus instead of the pathogen carrying the avr gene, the host would carry it and it could protect against highly virulent isolates.

The phenomenon of induced resistance offers great potential for engineering resistance against a range of fungal pathogens. This is a non-specific resistance induced by infection of the plant. For example, the infection of the lower leaves of tobacco with TMV leads to resistance against fungi, viruses, bacteria, and insects. Concomitant with this resistance a large number of proteins are synthesised within the plant, these include glucanases and chitinases (Garner *et al.* 1992). Resistance against *Phytophthora infestans* has been achieved by this mechanism. Potentially if we can identify the genes involved in the induced resistance we can develop strategies to turn on these responses rapidly in the event of an infection.

The defence responses in the host include activation of lignin and phytoalexin biosynthesis. The level of phytoalexins may be modified to confer resistance to fungal pathogens. It has been found that the activity of the enzyme isoflavone-2-hydroxylase regulates the amount of phytoalexin synthesis in chickpea cell suspensions. Increasing the activity conferred resistance to *Ascochyta pisi* (Lamb *et al.* 1992). Greater levels of resistance could be achieved by modification of the gene for increased expression.

Plants can be modified to produce new types of phytoalexins, thus conferring resistance against normally pathogenic fungal species. The phytoalexin resveratrol is synthesised by stilbene synthase in a single step from p-coumaroyl CoA and malonyl-CoA (Lamb *et al.* 1992). Introduction of the stilbene synthase gene into tobacco caused the synthesis of resveratrol in tobacco.

There are now a number of strategies emerging for the genetic engineering of plants resistant to fungal diseases. The impetus for this work is the lack of alternative control measures. In many cases there are simply no natural sources

of resistance, and no effective fungicide treatments for control of the pathogen.

Integrated control

Integrated control will become increasingly important, especially as our understanding of interactions between host plant, pathogen, biological control and environment improves. However, the range of strategies available for integrated control in native plant communities are not as diverse as those in broad acre agriculture or horticulture. It is possible that an advantage of integrated control is the synergistic effect of combining practices (Coffey 1991). In intensive agriculture, many of the success stories of pathogen control include the incorporation of breeding strategies and chemicals, cultural and biological applications. However, integrated control is not a panacea for pest and disease control but an ecological approach to maintaining plant health (Kendrick 1988).

Existing control strategies of pathogens in natural plant communities in south-western Australia

Phytophthora species

The main control strategies for *Phytophthora* species in Western Australia have centered on *P. cinnamomi* and include hazard rating, assessment of risk, hygiene and quarantine measures, unfavourable to the pathogen but enhancing host resistance (Shearer & Tippett 1989). Hygiene includes planning, training, and exclusion methods such as strategic road placement, washdown facilities between infected and non-infected sites, confining activities such as logging to periods of least risk and strategic road management (Shearer & Tippett 1989). Management strategies which are unfavourable to the pathogen can also be effective. These include the manipulation of understorey by reducing *Banksia grandis* by fire or stump poisoning which reduces a potential source of inoculum. Fire can also stimulate *Acacia* growth, specifically *A. pulchella*, which has been shown to suppress *P. cinnamomi* activity. Chemical and biological control can also be used and have been discussed previously.

Until it is clearly established whether other *Phytophthora* species are endemic or not, strategies used for the control of *P. cinnamomi* may or may not be effective for these other species. Currently, detailed studies are being undertaken on *P. citricola* (F Bunny, *pers. comm.*) and *P. megasperma* (S Bellgard, *pers. comm.*). Both these species are homothallic and undergo sexual recombination which can add additional complexities to control compared to *P. cinnamomi* which is heterothallic. *P. citricola* is most frequently isolated from areas of disturbance such as mine rehabilitation, log landings and drainage lines (F Bunny, *pers. comm.*). Oospores have always been assumed to be important survival structures formed in soil and host plants. However, it is only recently that they have been shown to be produced in nonsterile soils. Oospores are now known to survive for a minimum of months in field soils which indicates their importance as survival structures. It is now almost certain that *P. citricola* is endemic in the jarrah forest (F Bunny, *pers. comm.*), and this is likely to be true for other areas of the south-west. Therefore, it is extremely important to increase research into the ecology and pathology of *P. cinnamomi*.

The importance of *Phytophthora* species as damping-off pathogens in natural ecosystems must not be discounted. Recently, it has been shown that *P. citricola* can behave as a post-emergent damping-off pathogen in mine rehabilitation (Woodman 1993). Therefore, additional research is required to ascertain whether *P. citricola* and other *Phytophthora* species can cause damping-off, especially in areas of disturbance (drainage lines, road verges, salt effected, waterlogged, fire damaged).

It is also important to consider that the ecology and pathology of a pathogen may differ in different environments. This has been shown with *P. cinnamomi* in rehabilitated mines. The mining process changes the soil environment substantially. Recently, extensive excavations of 1-6 year old *E. marginata* growing in rehabilitated mines and exhibiting early symptoms of infection have clearly shown that *P. cinnamomi* infects the collar and lignotuber region in preference to roots. With time the pathogen moves down into the roots and up the stem. Over 30 jarrah trees have been excavated, and at no time has *P. cinnamomi* been isolated from roots of trees exhibiting symptoms of early infection (Hardy *et al. unpublished data*).

The eradication of *Phytophthora* infections on woody plants by the use of chemicals has been shown to be almost impossible on plants growing in infected soils or container mixes, due to the formation of resistant survival structures such as chlamydospores and oospores (Ribeiro *et al.* 1991). In addition, a range of *Phytophthora* species, including *P. cinnamomi* and *P. megasperma* in plantations of *Abies procera*, *Pseudotsuga menziesii*, *A. magnifica* var. *shastensis* and *A. grandis* in the north-western United States could not be effectively controlled (Ribeiro *et al.* 1991). In contrast, infection of apple trees with *P. cactorum* could be eradicated/cured with the systemic fungicides metalaxyl and fosetyl-Al however, repeated applications were required (Ellis *et al.* 1986, Orlikowski *et al.* 1986). Therefore, fungicide application in natural ecosystems is unlikely to be effective in the long term, even if the costs of the fungicides and their application is not taken into account.

Stem and branch cankers

The distribution of canker fungi has mainly been ignored in all natural environments of the lower south-west. This is despite the observed increased incidence since the 1970's of eucalypt die-back decline (Kimber 1980). A number of pathogenic fungi have been associated with cankers of stem and branches of forest trees in south-western Australia (Davison & Tay 1983), and in heathlands and woodlands (Murray *et al. unpub. obs.*). Recent work on *Diplodina* (anamorph, *Cryptodiaporthe*) canker on *Banksia coccinea* suggests that this fungus is endemic (Shearer 1994) The outbreak of this fungus as a major pathogen indicates that some change in the biological balance of the system has changed. Schoeneweiss (1975) has associated disease caused by canker fungi to be aggravated by transient stress factors, such as excessive heat or waterlogging.

Murray, Wills & Hardy (*unpublished data*) examined 1259 cankers on 508 native plants, 49 different genera of fungi were isolated, of which putative pathogens included *Botryosphaeria ribis*, *Diplodia mutila* (teleomorph *Botryosphaeria stevensii*), *Endothiella* and a species of *Diplodina*. However,

B. ribis and *D. mutila* were isolated respectively, from 53 plant species in 24 genera and 23 species in 13 genera, which indicates their broad host range. In addition, a wide range of fungi were isolated from stem and branch cankers of plants grown on rehabilitated mines (Carswell 1993). Pathogenicity testing proved many of these to be pathogenic. It is likely that conditions in rehabilitated or other severely denuded sites (lack of canopy cover, high or low moisture levels and reduced plant diversity) could predispose plants to canker or other pathogenic fungi.

Armillaria luteobubalina.

Armillaria luteobubalina is a primary pathogen widely distributed throughout the south-western Australia; it is a native pathogen that infects a wide range of plant species from diverse families (Pearce *et al.* 1986; Shearer & Tippett 1988). It has been isolated from wandoo, jarrah, and karri forests as well as throughout the coastal fringe from Cape Arid up to Cervantes (Shearer *et al.* 1994). In the jarrah forest, the impact of this pathogen varies between plant community and climatic zone (Shearer & Tippett 1988). Control has been effective in certain instances with other wood rotting fungi such as *Coriolus versicolor* and *Stereum hirsutum* (Pearce & Malajczuk 1990, Pearce 1990). These wood decay fungi were shown to significantly reduce the invasion of *Eucalyptus diversicolor* stumps by *A. luteobubalina*. However, there are at present fewer options for the control of *A. luteobubalina* than those available for *Phytophthora*.

Conclusions

It is necessary for extensive and detailed surveys to be initiated to increase our knowledge of the identity and incidence of pathogens causing disease in the natural plant communities of the south-west of Western Australia. Detailed studies of pathogen survival, reproduction and spread as well as host infection and susceptibility need to be undertaken. Each pathogen and its interactions with each of its hosts must be considered individually. In turn, these need to be related to interacting factors such as environmental changes, insect associations and the influence of human activities. A comprehensive understanding of the pathogens present, their life cycles and how they are influenced by environmental and human interactions will help ensure that our management of these native ecosystems is effective. Consideration must be made to ensure that management practices do not consider a few pathogens to the exclusion of others.

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Future ecosystems — use of genetic resistance

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Abstract

Genetic resistance of jarrah to *Phytophthora cinnamomi* has been identified by glasshouse testing and validated by field trials and analysis of plant/pathogen interactions. Resistant lines of jarrah can be micropropagated and used for revegetation of bauxite mine-sites and have potential for use in replanting dieback graveyard areas in the forest. Experiments are underway to determine the level of resistance of the progeny of selected resistant trees. Several questions are posed in this paper on the use of genetically resistant plants in restoring ecosystems.

Introduction

We have shown that it is possible to select *Eucalyptus marginata* (jarrah) resistant to *Phytophthora cinnamomi* and that this resistance is genetically based. A number of jarrah trees were selected on the basis of their apparent field resistance or susceptibility to *P. cinnamomi*, or because they represented an ecotype of jarrah. At 12 months of age, half-sib seedlings were screened for their reaction to the pathogen using underbark inoculation or by inoculating the soil. The mean lengths of the lesions, or the percentage of plant deaths, were used to rank families (*i.e.* progenies from individual open-pollinated mother trees) from most resistant to most susceptible (Stukely & Crane 1994). From the extremes of the range, highly resistant plants from resistant families, and susceptible individuals from susceptible families were chosen and micropropagated (McComb *et al.* 1990).

The clonal plants were planted in dieback-affected sites on rehabilitated bauxite pits and were inoculated with 4 strains of the fungus 1 month after planting. After 5 years in a typical field trial, the resistant plants have shown a low number of deaths and excellent growth, while in some susceptible lines all the plants have died (Fig 1).

Laboratory testing of the selected plants has shown that, after infection of root tips with zoospores, the resistant jarrah plants confine the lesion extension; this was also observed in roots of the field resistant species *E. calophylla* (Cahill *et al.* 1992). Further work is underway to investigate the mechanism of this resistance and its interaction with environmental variables such as temporary waterlogging (Cahill & McComb 1992, Cahill *et al.* 1993).
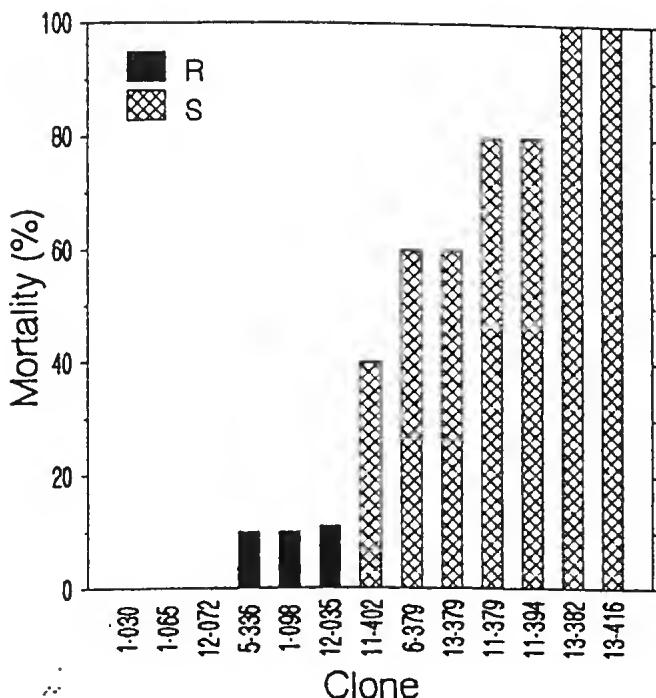
Figure 1. Mortalities of *Eucalyptus marginata* clones derived from seedlings resistant (R) and susceptible (S) to *Phytophthora cinnamomi*, after 5 years of growth in a *Phytophthora*-infested bauxite mine-site.

Heritability of resistance to *P. cinnamomi* was estimated from analysis of mortalities after soil inoculation in pots and in the field, and from stem lesion lengths after underbark inoculation of 15 - 50 half-sibs from each of 16 families (Stukely & Crane 1994). Resistance to *P. cinnamomi* was found to be under strong genetic control as narrow-sense heritability for the families was 0.74 - 0.85 and for individual trees was 0.43. We are studying the inheritance of the resistance trait further by controlled crosses and will gain information on other characteristics such as flowering times and combining ability for resistance.

Can genetic resistance to *P. cinnamomi* help restore damaged ecosystems?

It is important to investigate the use of resistant clones of jarrah to re-establish the species in areas in which it has died from dieback, that is on graveyard areas. This will be a greater challenge than the establishment of clones in bauxite pits where root competition is absent, drainage is optimised and the soil is friable. We have yet to develop reliable techniques for establishing micropropagated plants in graveyard areas where jarrah plants have to be inserted between existing vegetation, and it is not possible to provide the same level of site preparation as in bauxite pits.

In the ideal situation, the trees that are used in graveyard plantings will eventually establish a self-sustaining population of largely resistant trees. This will only be possible if we can identify clonal lines with good combining ability for resistance, and these lines flower at the same time.

In restoring a damaged ecosystem we feel it is necessary to utilise, as far as possible, genotypes from the surrounding forest. With this in mind we are now doing further selections from the northern and southern regions of the jarrah forest. However, jarrah is just one species which is killed in natural ecosystems. Replacing the jarrah is a small step towards reversing the floristic impoverishment of the affected areas.

Can the method used for selection of resistant jarrah work for other species and other diseases?

Theoretically it would be possible to screen other plants with *P. cinnamomi* or other pathogens and to find resistant individuals in the field. However, on some forest sites jarrah is relatively resistant to *P. cinnamomi* (Dell & Malajczuk 1989) compared with many other species, in which there may be 100% deaths. There are problems too, not only with the vast number of species that are affected in each ecosystem, but also the length of time required to work out reliable propagation or micropropagation methods for some species, and to develop appropriate screening methods. Clearly it is a strategy only suitable for priority species. It may be possible to partially restore an ecosystem by use of selected resistant lines of a restricted number of species. This would at least provide more diversity of plant species and animal habitats than are found at present in graveyard areas.

Can the new techniques of genetic markers or probes make selection of disease resistant plants faster?

In some plant / pathogen interactions it is now possible to identify disease resistant plants by extracting the DNA and probing it for DNA sequences known to indicate resistance. It is not necessary to know the mechanism of the disease resistance and the technique allows screening of plants from disease free areas and of plants whose propagation is difficult.

This exciting development must be underpinned by initial work in each species to identify some resistant and susceptible lines and some study of the heritability of resistance. However, once appropriate markers are found, screening for suitable resistant individuals for seed orchards, vegetative or micropropagation can proceed more rapidly. The technique is likely to work most quickly when there are major genes for disease resistance, but it may also be effective in polygenic systems of resistance such as in jarrah.

Can natural resistance be enhanced or replaced by genetically engineered resistance?

Genetic engineering offers almost unlimited scope for introducing novel mechanisms for disease resistance into plants. In practice, the problems of working out appropriate techniques for introducing new genetic material into a number of species in a natural ecosystem are immense and consequently very costly. Added to this are ethical problems. There may be few objections when the introduced gene is from a resistant plant of the same species, but we might expect objections when genes from unrelated organisms are used.

Genes introduced by genetic engineering may come from unrelated organisms and in recipient species they form new loci usually dominant in expression. In a cross-pollinating species with a short generation time and under high selection pressure, the gene would spread quickly through the population. Are we willing to see this type of genetic engineering in our natural ecosystems? Is the damage from *Phytophthora* and other pathogens so great that we would be willing to make the natural ecosystem, to some extent, unnatural ?

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Future ecosystems — ecological balance (ecological impact of disease causing fungi in south-western Australia)

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Abstract

Ecosystems are dynamic not static; however, since European settlement the rates of change have been dramatic and rapid. Entirely new types of disturbances have occurred including land clearance, new grazers, new predators, new pollinators, new weeds and new diseases. All of these have impacted on the ecological balance of native plant and animal ecosystems, and their effects are synergistic not unique.

South-western Australia has unique species-rich and structurally diverse plant communities, supporting a web of co-evolved fauna species. New plant diseases may lead to simpler ecosystems in terms of structure, diversity and function. Remnants will often be severely impacted, and more prone to weed invasion. Larger areas may become dominated by fewer resistant species.

Many susceptible plant species of restricted ranges face the possibility of extinction in the medium term. More widespread susceptible taxa face severe genetic erosion through local extinction of populations in remnants where re-invasion is not possible. Native animal species which rely on the floral diversity for food and shelter may face local extinction, or at least critical reduction in numbers.

Perhaps the greatest challenge facing land managers and those attempting to conserve our wild heritage is to understand, detect and lessen deleterious disturbances from completely overwhelming our remaining bushland, and rendering it more vunerable to disease.

Introduction

All ecosystems are dynamic and change in place and composition over time. Disturbance is a recognised feature of ecosystems, and appears to be vital in maintaining species and community diversity. However, prior to the advent of industrialised European man, this cycle of disturbance and renewal occurred in a setting of continuous bushland. Since settlement in Western Australia and the clearing of land for agriculture, all ecosystems have been rapidly and severely impacted. In the south-west of Western Australia the major change has been the fragmentation of the bush by clearing for other land uses. This has resulted in numerous, often small, isolated bushland remnants many of which appear to have a limited future without careful management. Clearly, fragmentation of ecosystems and its consequences are major challenges facing conservation managers world-wide.

Disease is one aspect of natural population control involved in disturbance and change, but combined with fragmentation it may prove decisive, destructive and unidirectional. This paper mainly deals with *Phytophthora cinnamomi*, but it should be noted that several other diseases briefly mentioned here also pose local severe conservation problems and deserve closer scrutiny.

Impact

Root cankers:
Phytophthora cinnamomi

Detailed studies in Victoria (the most climatically-similar area) in dry sclerophyll woodlands, heaths and swamps in the Grampians, Brisbane Ranges and Wilsons Promontory by Dawson *et al.* (1985), Kennedy & Weste (1986), Weste (1975, 1981 & 1986), Weste & Law (1973), Weste & Taylor (1971) and Weste *et al.* (1973) have shown that the disease has permanent and severe effects on the structure and floristics of these plant communities. Similarly severe and permanent impacts have been noted in Tasmania (Podger *et al.*, 1990) and Western Australia at Two Peoples Bay (Hart 1983), Cape Arid and Cape Le Grande (Brandis *et al.* 1985), Stirling Range (Wills 1993), the jarrah forest (Shearer & Tippett 1989) and the Banksia woodlands of the Swan Coastal Plain (Podger 1972, Shearer & Hill 1989, Shearer 1990). Potentially major impacts can be expected in the heathlands north of Perth (Hill 1990), and in the understorey of many communities of the southern forests (Shearer 1992). The western edge of the wheatbelt and localised populations of proteaceous heaths in suitable catchments in this entire region could also be at risk.

In general, the ecological balance which might be achieved in future ecosystems after major disease impact is likely to be reflected in simpler communities in either structure (loss of susceptible dominants) and/or floristics (loss of susceptible species), hence a net local loss of biodiversity. These effects

are most widespread and severe in the south coast heathlands of Western Australia, from Augusta to Cape Arid. Since this region also contains the highest proportion of vertebrate pollinated flowering plant species in the world (Keighery 1982), many of which are Proteaceae, and susceptible to dieback, secondary effects will also be severe on the diversity of animal communities (Friend 1992) in this area.

Bird-pollinated plants often dominate our flowering heathlands in spring, with their large and brilliantly coloured flower; many of these species are highly susceptible to dieback and are replaced by wind-pollinated resistant sedges, a dismal sight to any honeyeater or tourist. Dieback is likely to reduce local populations of these birds. Insects reliant on susceptible species will also face significant reductions in food sources (*e.g.* the specific bee pollinators, *Leioproctus pappus* of *Conospermum incurvum*, *Euryglossa morrisoni* of *Verticordia nitens* and *Euryglossa aurea* of *Verticordia aurea*; Houston 1992), but there are few data on the extent of this aspect. The effects on soil organisms, including fungi (see Malajczuk & Pearce 1994) is almost completely unknown, but it must be considerable.

The second major impact will be on the hundreds of bushland remnants containing susceptible communities in an arc between Moore River, Kojonup and Esperance. In the studies noted above, the affected areas are within large areas of native vegetation, enabling immigration of resistant taxa, with refuge areas often present for susceptible taxa. In small isolated remnants there is little chance of recruitment from neighbouring remnants, no refugia and local extinction is the major consequence, accompanied by weed invasion. For example, the Swan Coastal Plain Survey has placed over 500 permanent vegetation quadrats in bushland between Gingin and Dunsborough, and has compiled total flora lists for most reserves in this area and on sections of the escarpment. Quadrats at Twin Swamps, Bullsbrook, and Cardup Nature Reserves, shown a major decline in species diversity in communities invaded by *Phytophthora cinnamomi* and a major increase in weed invasion following severe impact by *Phytophthora*. Average species diversity declined from 69 species to 39 at Cardup or from 49 to 25 at Twin Swamps, and weed species increasing from an average of less than 2% to over 50% of species records at some sites in Twin Swamps. The disease removes susceptible dominants and understorey species, hence opening the community to invasion by resistant annual and grassy weeds. Flora surveys indicate that local extinctions of many susceptible understorey taxa such as *Banksia meisneri* var *adscendens*, *Verticordia nitens* and *Lambertia multiflora* var "darlingensis" are likely to occur over the next 5 years at Ruabon, Bullsbrook and Cardup Nature Reserves respectively unless urgent remedial action is taken. Remnants with service corridors through them or with wetlands in or adjacent to the remnant appear to suffer the highest impact, with disease spreading from the wetland or corridor. These remnants are likely to lose their Banksia woodlands entirely, as the dominant Banksia trees become locally extinct. At a species level, the disease has the potential to lead to at least the localised extinction of highly susceptible species.

A number of recent publications list and publicise the taxa under the greatest threat (Conservation and Land Management 1992, Curry 1992, Curry & Kelly 1993, Keighery 1988 a, b, 1991, 1992). Eleven taxa are under greatest threat

with most or all populations infected (Table 1). Seven of these are considered under threat of extinction in the wild, and the four other taxa are being monitored to determine their status and management options.

Table 1
Taxa requiring urgent management action to lessen the impact of Phytophthora

A) Taxa under threat of extinction in the wild in the medium term, all populations impacted by disease:

Andersonia axilliflora
Andersonia sp (Two Peoples Bay)
Andersonia sp (Mt Lindesay)
Banksia brownii (Both forms)
Dryandra "montana"
Isopogon uncinatus
Lambertia echinata

B) Taxa with most populations infected by disease, potentially at risk of extinction in the wild:

Calytrix breviseta ssp *breviseta*
Conospermum caerulescens ssp "adpressum"
Dryandra sp 30
Lambertia orbifolia

Current research and management has centred on protecting stands of the most threatened species (currently *Andersonia* species and *Banksia brownii*) by phosphonate spraying and collection of germplasm material (of all taxa) for *ex situ* long term storage. *Ex situ* germplasm collections are a last resort but in a number of cases may be the only means of preventing total extinction of a species. Information on the effects of disease on many other restricted and potentially threatened species, such as the mountain bells (*Darwinia* species), *Adenanthos detmoldii*, *A.pungens*, *Persoonia micrantha*, *Isopogon uncinatus*, *Banksia occidentalis* ssp. *formosus*, and *Petrophile latericola*, is urgently needed to set priorities and develop strategies for their conservation and management. More widespread susceptible species, such as *Banksia coccinea* and *Lambertia propinqua*, are suffering significant genetic erosion through the local extinction of populations and reduction in population size. Other species such as *Lambertia orbifolia*, *Banksia brownii*, *Banksia ilicifolia* and *Adenanthos barbigerus*, are in danger of losing genetically and morphologically distinct races. Again the ecological balance is being shifted to less complex communities, by the loss of regional genetic and specific diversity (geographically restricted taxa and localised population divergence appear to be a feature of plant communities in south-western Australia; Hopper & Coates 1990).

Other *Phytophthora* species

Five other species of *Phytophthora*, namely *P. citricola*, *P. cryptogea*, *P. dreschleri*, *P. megasperma* and *P. nicotiana* have been identified from dead and dying native vegetation. All of these species can have localised severe impact, and probably pose a major threat to at least some local populations of susceptible flora (such as the localised, declared rare species, *Adenanthos ellipticus* on East Mt Barren) and isolated remnants.

Wood rots

Armillaria luteobubalina is the major species of wood rot, with a wide and diverse host range, often from groups resistant to *P. cinnamomi*, and in habitats usually at low risk from root rots *e.g.* Coastal dunes and Spearwood sands (Shearer & Tippett 1989). The impact of disease caused by this fungus on a local scale in Granite heath, Wandoo and Coastal heath can be severe, hence its greatest impact will be on remnants, where it may cause local extinctions and enhanced weed invasion. Localised rare species could also be at risk. Detailed long term studies are required on the effects of this disease, since it is a native species, to understand its role in native plant communities.

Stem and branch cankers

Currently the major concern is the canker *Cryptodiaporthe* sp. which affects a broad range of Proteaceae, often causing death of the plant. *Banksia coccinea* populations are being heavily impacted by this canker, and this species faces localised extinction in the Albany area. The only known population of *Dryandra* sp (Kamballup) is infected with canker (Wills, *pers comm*), and requires monitoring. A series of other cankers can cause dieback and death and loss of overstorey Eucalypt species, including Marri and Red Flowering Gum, Wandoo and Tuart. These diseases could prove severe in remnants, preventing the replacement of species after loss of the parental trees. These cankers appear to be a response to various types of disturbance and/or enviromental factors such as drought stress, and their long term impacts are unknown.

The future

The symposium organisers requested that we speculate, based on current knowledge what the ecological balance of future ecosystems would be under current trends of diseease spread and impact. Our potential future is major impacts of these diseases in south western Australia, as presented below.

The combined fragmentation and increasing levels of disturbances will inevitably result in a loss of biodiversity. This will result, through the changes in community structure favouring resistant species, in the extinction of local populations of numerous species and the subsequent loss of genetic diversity, the likely extinction of many rare and geographically-restricted susceptible species, secondary species loss of both plants and animals through lack of pollinators, food plants and shelter, severe genetic erosion of widespread susceptible taxa, and a loss of scenic values to the public and tourists. Currently the ecological balance seems to be shifting towards simpler, weed-invaded and less visually appealing plant and animal communities, that may lack many of their uniquely Western Australian features. There seems little doubt that introduced diseases are hastening this trend.

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The future — effects of plant disease on society

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Abstract

Just as humans react adversely to too many changes occurring too rapidly, many plant species of the south-west of Western Australia will not withstand the rate of change in their environment. There are many ways in which the structure and composition of plant communities are being drastically altered over large areas. Plant diseases may well express as never before. Disease epidemics may be one of the things which force changes in the way the ecosystems of the south-west are managed and utilized. Management should be based more on basic ecological principles and less on economic considerations. Much greater emphasis should be placed on disease prevention. It must be realised that many systems of disease control developed for horticultural situations are not applicable for broad scale use in natural ecosystems. Once management is more in accordance with basic ecological principles, there will be less conflict in society between those who are fearful for the future health of south-western ecosystems and those who believe "the bush", the forests in particular, will withstand intensive exploitation and repeated disturbance.

If disease prevention does not become a prime objective of management, future generations will get fewer and fewer opportunities to appreciate, exploit and enjoy the great diversity, complexity and beauty of the ecosystems of the south-west, which Europeans discovered less than 200 years ago.

Effects of plant disease on society

Future effects of plant disease on society will be numerous. There are the obvious things; more regulations, more expensive natural products and decreased supply of products previously, all taken for granted. One less-obvious effect will be a greater divergence of management techniques used in natural ecosystems from those used in areas of intensive production such as on farms and in plantations. Plant diseases are difficult and often impossible to control in natural ecosystems; for example the root diseases caused by *Phytophthora cinnamomi* and *Armillaria luteobubalina* can be either prevented or controlled in horticultural situations, but both are almost impossible to control in conservation and forest areas where there are numerous infections spread over vast areas.

The incidence and severity of plant disease in our south-western ecosystems are going to increase and as a consequence the ways of management will be forced to change. There has to be much more emphasis on disease prevention. Society must be much more honest about the long term objectives of management of both the conservation estate and forests. Economic rather than ecological principles are primarily determining how the ecosystems of the South-west are currently being managed. Some plans are initiated from a base of ecological information but then debased by extrapolation over vast areas of widely varying communities; for example jarrah logging prescriptions and the treatment of mixed species Eucalypt forests.

This paper is too short to discuss the factors which favour the development of plant diseases in detail. Shearer (1992)

suggested many ways in which human activity could either aggravate or control disease in forest ecosystems. I believe there is plenty of evidence that disease incidence and severity will increase as a consequency of human activity. Society seems to be doing much more to encourage plant diseases than to prevent or suppress them. Of particular concern to me is the rate of logging in State Forest. Disease prevention seems to be a low priority.

The case for woodchipping and clear-felling is in part based on the ability to regenerate karri forest from seed and seedlings. The ash type eucalypts lend themselves to such management especially when they are in relatively pure stands but there are fewer and fewer stands with predominantly karri available for clear-felling. Much of the forest being treated as karri has few stems of karri per hectare; the rest is marri, blackbutt and jarrah. Much of it is essentialy jarrah forest. What is of concern is that karri is being established back on to many areas and soil types where it never grew naturally at high densities. We are imposing a plantation-type system within natural ecosystems without the knowledge or resources to manage disease. The incidence of brown wood and incipient rot is high in regenerated karri stands (Davison & Tay 1994, Shearer 1992). The stability and benefits of mixed species stands are not understood. Across Australia, often a species of the *Eucalyptus* sub-genus *Monocaplytus* and a species of the sub-genus *Symphomyrtus* seem to form stable associations (Boland *et al.* 1984).

The recently approved Forest Management Plan 1994 - 2003 (Conservation and Land Management 1994) for this State will mean that areas of jarrah forest, in the order of 130 km^2 to 300 km^2, will be "clear-felled" every year and require ongoing thinning. Many of the areas so treated will be in the low and intermediate rainfall zones of the forest where the quality of forest is mixed and little research has ever been done. The recent past scale of the operations means that there is already something like 4126 km^2 of regenerating jarrah

forest, with less than 20 years of growth (figures collated from Forest Department (WA) and Conservation and Land Management Annual Reports).

As stated by the Environmental Protection Authority (1992), the commitment to the type of management described in this paper "would lock the state into long term acceptance of the new forest structure and the new intensive production with insufficient flexibility to adapt management in the light of new information or changes in community expectations". What does happen if, as I predict, diseases hinder regeneration and growth rates do not meet levels set in computer models? I believe that there are already quite inadequate resources to guarantee a healthy crop of trees over all of the areas being logged. Intensive monitoring and disease mangement seems even less likely.

Forests are slow to grow and conversely they are slow to die. Consequently, mismanagement may take 20 to 40 yrs to express on a large scale. The danger is that economics rather than ecological principles will drive management of forests for too long and signs of decline will be ignored. Unfortunately, a single State Department controls most of our natural ecosystems and one disadvantage of this state of affairs is that "blanket" prescriptions are imposed over vast areas. When mistakes are made, the consequences will be great. In industries where private enterprise flourishes, many ideas are tried on a small scale all the time. Those that are not any good, fail, without great cost to society.

Society must honestly address the question of sustainability and what of the natural ecosystems of the south-west will be left to provide future generations. Multiple use of areas means increasing pressures on the vegetation. The frequency of disturbance, including fires, is ever increasing, presumably resulting in effects such as decreasing numbers of mature seeding plants and decreasing carbohydrate reserves within perennials. How do we measure the potential of different plants and communities to reproduce, recover and resist disease after repeated disturbance? We have few measures of vigour or resistance. Slow and gradual decline of species is also difficult to monitor. The decline of species is often masked by the colonization of bare ground by other species. Even with dieback caused by *P. cinnamomi* few people appreciate the extent and changes in the floristics of plant communities in the south-west because *Agonis* species and rushes have replaced many of the species killed. Surely one of the things about planning for the future is heeding warnings. Warnings can result from monitoring. There has been far too little monitoring done in vast areas of the south-west on dieback or anything else. The effects of disease on regeneration of dominant species should surely be a high priority? What are the effects of *P.cinnamomi* on jarrah regeneration on different soils?

Usually a crisis has to be well documented before politicans will respond. Plant disease epidemics along with insect plagues will help sway society to call for change. At least the conservation estate should be managed in accordance with basic ecological principles. Compromises, a result of too many conflicting pressures, should be sought warily.

I believe that, once ecological principles are the basis of vegetation management, there will be less conflict in society between those who believe, "the more you bash it the better it'll be" and those who do have a degree of understanding of the complexity and vulnerability of the ecosystem of the south-west. At least the forest debate could become less polarised. I believe community expectations of sound management of our natural ecosystems are going to ever increase. In the future, the public will be better educated in environmental biology and as more environmental disasters become apparent their assessment of management practices will be more and more rigorous.

The current education curricula in schools are stressing an understanding of environmental issues such as dieback and salinity. The general level of appreciation of the flora and fauna is increasing and people will be more sensitive to adverse changes brought about by plant disease. When people go out and plant trees in "greening" programmes and they die, some will ask why?

More people will observe and recognise problems as they arise. Society must appreciate the ecosystems on which it impinges, including their complexity and vulnerabity; otherwise there will not be the will and determination to minimize the impacts of disease.

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